Comparative Insights Into Convergent Evolution

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Summary

Evolution has traditionally been seen as an open-ended, adirectional process. However, the ubiquity of convergent evolution instead suggests that a hierarchy of physical and biological constraints shape evolution. This thesis examines the empirical evidence for convergent evolution's impact on macroevolutionary patterns.

One corollary of convergent evolution is the tendency for animal groups to reach maximum morphological disparity early in their evolutionary histories. An analysis of plants confirms that bottom heavy disparity profiles (Centre of Gravity < 0.5) are not unique to animals. This pattern is most easily explained by character exhaustion, with repetition of character states becoming increasingly probable as evolutionary time increases. However, in a sample of 93 extinct clades, no correlation between character exhaustion and disparity profile shape was found. Instead, ecological or genetic constraints likely limit organism form.

Convergent evolution can introduce noise to morphological phylogenies. Anecodotal evidence in mammals shows molecular phylogenies are more congruent with biogeography than their morphological forbears, suggesting ecological constraint could be driving morphological convergence which confounds phylogeny. Similar patterns are common in other clades. In a systematic study of 48 plant and animal clades, the significant majority (70%) of molecular trees were more consilient with biogeographical distributions than their morphological counterparts.

Genetic constraint might also limit evolutionary possibility and drive convergent evolution. If so, genome duplications, by introducing genetic redundancy, are expected to be associated with evolutionary novelty and diversification. An analysis of 356 sister clade pairs shows polyploids contain significantly more species than their non-polyploid counterparts. Whilst a direct link between morphological and genetic constraints has yet to be identified genetic constraints are likely to play an important role in the diversification of species.

Finally, the importance of these findings for the study of convergent evolution and evolutionary processes in general is discussed, along with future lines of research.

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1 Introduction

Evolution has traditionally been seen as an open-ended process with the potential to give rise to a near-unlimited range of forms. This tradition is now being challenged by a new view which recognises evolutionary potential may be limited, to varying degrees, in most cases. Authors often cite numerous examples of convergent evolution as compelling evidence for this new view of evolution. Convergent evolution is characterised as the development of identical features or traits from independent origins. While convergence appears to be widespread, there have been few studies which have sought to compare its effects or prevalence across groups. This thesis will attempt to compare some of the most significant hypothesised consequences of convergence across a wide range of plant and animal clades to determine what, if any, general rules of convergence exist.

1.1 Understanding Evolutionary Pattern & Process

1.1.1 Similarities, Differences & Darwinism

Naturalists, from ancient times right up to the days of Darwin have focused on explaining and categorising the diversity of life. While the taxonomic work of Linnaeus and others (Linnaeus 1758; Raven et al. 1971) was concerned largely with categorising and recognising patterns of organisation in living organisms, others sought to provide mechanistic explanations for how these patterns came to be (Lamarck 1809; Haeckel 1866; Tassy 2011). Ever since the theory of evolution by means of natural selection, proposed by Charles Darwin and Alfred Russell Wallace (Darwin 1859; Wallace 1871), many evolutionary biologists have focused on explaining how the life we see is different in so many aspects (Stebbins 1950; Burns et al. 2002; Charlesworth 2009). However, if evolution is a process of infinite variety one must also consider how the widespread phenotypic similarities used by taxonomists can develop. Darwin provided an elegant explanation; more closely related species are more likely to retain the same characteristics from their common ancestor. He also understood that this pattern wasn't universal, as distantly related species could possess similar organs. He cited as examples the electric organs of fish (Gallant et al. 2014), luminous organs in insects (Widder 1999) and pollen aggregation in flowering plants (Harder and Johnson 2008) as being particularly difficult to explain. It was not just Darwin who recognised this type of

convergent evolution, many comparative anatomists of the time also appreciated that similarities in form did not necessarily reflect common ancestry (Appel 1987). This was thrown into a particularly stark light with the discovery and study of the fossils of strange animals and plants that defied known Linnaean classifications. It was in part these fossils which spurred British palaeontologist and comparative anatomist Richard Owen to formalise this distinction with his definitions of homology and analogy (Boyden 1943). While homologous traits owe their similarity to inheritance from a common ancestor regardless of function (e.g. the paddle limb of a water boatman and a stick insect leg), analogous traits only appear similar because they share a similar function (e.g. limbs in insects and tetrapods). In publications which followed in the late 1800s and early 1900s explanations for these analogous traits largely focused on the importance of natural selection, detailing common adaptations to similar ecologies or environments, (Eigenmann 1905; Lull 1906; Muir 1923).

1.1.2 The Neo-Darwinian Framework

Although biologists postulated that natural selection acted on heritable traits, it was the rediscovery of Gregor Mendel's work in 1900 that provided a mechanism by which traits could be inherited. These 'inheritable units', later termed genes, were the foundation of Mendelian genetics and had a profound impact on the formation of evolutionary biology as a modern scientific discipline (Carlson 2004). Later workers, notably R.A. Fisher (Fisher 1930), put Mendelian genetics within a modern statistical framework and expanded it into the discipline of population genetics. For the first time, predictions of evolutionary theory could be tested quantitatively. These studies were complimented by Ernst Mayr's articulation of the biological species concept and theories of speciation, which emphasised the importance of reproductive isolation in giving rise to species (Mayr 1942). Most explanations of evolutionary change still very much centred on adaptation to new environments. The work of G. Ledyard Stebbins eloquently and powerfully articulated many of these ideas and applied them to plants (Stebbins 1950), focusing on speciation through hybridisation (Anderson and Stebbins 1954) and adaptive radiations, in which organisms rapidly diversify into a range of forms to take advantage of new resources or environments (Stebbins 1959). While evolutionary geneticists such as Theodosius Dobzhansky concerned themselves with illuminating the importance of random mutation in natural populations giving rise to variation upon which selection can act (Dobzhansky 1937), palaeontologists such as George Gaylord Simpson were attempting to unite population genetics with the picture of macroevolution supplied by the fossil record (Simpson 1944). These advances were united in the 'modern synthesis' of evolutionary biology (Huxley 1942), a scientific movement that sought to use Darwin's ideas of natural selection and Mendel's ideas of inheritance as the theoretical core of the

quantitative study of evolutionary patterns and processes. What the modern synthesis added to our understanding of convergence and the evolution of phenotypic similarity was a greater appreciation of how similar environments or selective pressures could give rise to similar traits in distantly related lineages (Macarthur and Levins 1967).

Later in the 19th century, another important formalisation vastly improved our ability to identify convergently evolved traits, as Willi Hennig adapted many of the previous concepts of homology into a phylogenetic framework (Hennig 1950; Hennig 1966). His cladistic methodology centred around recognising which biological traits (termed characters in cladistics) were synapomorphic, that is, characters unique to a group of related organisms but present in all members within the group. Quantifying phenotypic similarity is therefore key to this approach, with the maximum parsimony criterion preferring the evolutionary tree that infers the fewest character changes (Kitching et al. 1998). In Hennig's terminology, characters which appear multiple times on a tree (which includes those which have evolved convergently) are homoplasies. Subsequent cladistic analyses have revealed that even when optimising under maximum parsimony the number of homoplastic characters is significantly higher than the number of synapomorphies in many groups (Sanderson and Donoghue 1989). This spurred interest in the evolution of specific homoplastic traits and in particular convergently evolved traits. Through more detailed study of how convergent traits evolve on phylogenies (Wille 1977; Wyss 1989), it became clear that distantly related organisms could evolve similar traits even in very different environments.

1.1.3 Evolution & Genetics

Throughout the latter half of the 20th century, large parts of the neo-Darwinian framework came to be viewed with increased scepticism because of advances in the field of genetics. There were primarily two significant developments that lead to this revision in evolutionary thought. The first was the development of and mounting evidence for the neutral theory of molecular evolution, which proposed that most genetic change occurred via stochastic processes rather than under the influence of natural selection. The second was the development of molecular phylogenetics which seriously challenged assertions that parsimony and morphological homologies would illuminate evolutionary relationships.

It became increasingly clear in studies of population genetics that most differences in the DNA sequences of organisms could be explained through relatively simple models of random mutation (Freese and Yoshida 1965). This was formulated into the neutral theory of molecular evolution by Motoo Kimura and others (King and Jukes 1969; Kimura 1983), which suggested that most genetic change was selectively neutral, citing as evidence the fact that most DNA base pair differences appear to have no effect on the selective

fitness of the organism (Crow 1970). In contrast to neo-Darwinian theory, the neutral theory proposed that most selection was not directional natural selection in the Darwinian sense, but purifying selection to remove deleterious mutations (Nei and Gojoborit 1986). Instead of selective pressures, the population size, the frequency of alleles in the founder population and the mutation rate determine the evolution of genes through genetic drift (Lande 1976). While the original neutral theory stated all mutations were either too deleterious to exist in the population or selectively neutral, a modification of the theory, the 'nearly neutral theory' scaled the effects of purifying selection based on a selection coefficient and the population size (Ohta 1973). At larger populations the effects of genetic drift are weaker and fewer alleles become fixed in the population. Subsequent studies found abundant evidence for selection at the molecular level (Doolittle and Sapienza 1980; Sueoka 1988; Hahn 2008). However, the neutral theory and its iterations were critically important in demonstrating that significant evolutionary change could occur over time without strong selective forces, therefore not all evolutionary patterns require an adaptive explanation.

The second revolution of genetics was the development of molecular phylogenetics and systematics, which provided a vast wealth of new data with which to analyse evolutionary relationships. The theoretical framework for much of molecular systematics was established in the 1960s (Margoliash 1963), and it was argued by several workers that molecular data represented 'more direct' evidence of evolution than morphology (Zuckerkandl and Pauling 1965a; Zuckerkandl and Pauling 1965b). However, for a number of reasons, it would be many decades before their ideas became a reality. Firstly, there was a fundamental miscommunication at the time between molecular biologists and morphologists about the nature of the data. While morphologists viewed protein molecules as single characters free from selection pressures (Kloz 1962), molecular biologists viewed proteins as being composed of many characters corresponding to amino acid residues (Peacock and Boulter 1975). Secondly, calculating the actual number of mutations that took place at a given nucleotide is not a trivial task (Lynch 2010). Thirdly, the DNA-DNA hybridization technique in use for most of the 1970s and 80s was criticised for being inaccurate when inferring relationships between closely related species as contrasting orthologous sequences were overwhelmed by hybridisation of paralogous sequences within the organisms (Sarich et al. 1989). During this time there were also controversies on the nature and significance of genetic variation. The so-called 'classical school' was slow to accept that genetic variation was high in wild populations. Proponents of this school of thought argued that genetic variability had a strong detrimental impact on the fitness of populations (termed 'genetic load'), possibly even resulting in extinction in extreme cases (Frankham 1998).

It wasn't until the mid-1980s that these arguments had, in large part, died down and Sanger sequencing methods (Sanger et al. 1977) became widely available enough to collect large volumes of sequence data. Utilizing this data in phylogenetic reconstruction required new mathematical models of sequence evolution, to both compensate for the high rate of replacement of amino acids or nucleotides and to make use of experimental evidence for the difficulty of certain changes relative to others (Yang 1996; Duret and Mouchiroud 2000). Both maximum likelihood (Yang 1994; Stamatakis 2006) and Bayesian inference (Larget and Simon 1999) methods of increasing sophistication have been developed to model rates of evolutionary change in sequences. This has led to extensive phylogenetic revisions in many groups of organisms which were often, to varying degrees, in conflict with previously established classifications based on morphology. As a result, convergence was revealed to be far more prevalent that any evolutionary biologist expected, as many previously hypothesised morphological synapomorphies were found to have evolved many times independently on the tree of life. In particular, remarkably similar traits were shown to have evolved independently many times in mammals (Parker et al. 2013; Gheerbran et al. 2016), birds (Fleischer et al. 2008; Felice and O'Connor 2014; Cooper and Uy 2017), reptiles (Kearney and Stuart 2004; Harrington and Reeder 2017) and insects (Pascoal et al. 2014; Berens et al. 2015; Faille and Pluot-Sigwalt 2015) in convergent specialisations to different niches.

1.1.4 Macroevolutionary Patterns, Predictability & Gould's 'Tape of Life'

Early work recognising the existence of patterns and trends in the fossil record dates to the end of the 19th Century and the neo-Lamarkian movement spearheaded by palaeontologists, most notably Edward Drinker Cope. Cope recognised the existence of strong, almost linear, trends in the properties of extinct animals. The most famous of these trends, the so-called 'Cope's Rule' for body size to increase in a lineage of populations over time was first explored by German zoologist and neo-Lamarkian Theodore Eimer in the 1880's, popularised by Charles Depéret in the early 20th Century and coined 'Cope's Rule' by Bernhard Rensch in the decades after (Polly and Alroy 1998). Around the time Cope's Rule was being popularised, Simpson's work on the evolution of mammals (Simpson 1944; Simpson 1945; Simpson 1953) encouraged evolutionary biologists to start to explore macroevolutionary patterns with increasing volumes of fossil spatial, temporal and taxonomic data. Simpson's view was that the mechanisms of microevolution which were the basis of evolutionary genetics could sufficiently explain evolutionary change over the entire history of life, which occurred mostly through steady phyletic change. However, as new molecular topologies elucidated more and more examples of convergent evolution which had previously remained completely undetected, some began to question whether these long-standing

ideas on how macroevolution operates were correct. Phenomena in the history of life such as mass extinction events (Hallam and Wignall 1997; Erwin 2001; Villier and Korn 2004; McElwain and Punyasena 2007) and large-scale diversity trends (Niklas et al. 1980; Foote 1991b; Sepkoski 1993; Miller and Foote 1996) became apparent for the first time, challenging scientists to fit the Neo-Darwinian model of evolution to these seemingly chaotic and grandiose patterns. More so than ever before, the fossil record revealed the long and complex history of life on earth, a history filled with the recurrent evolution of the same methods of locomotion (Lingham-Soliar and Plodowski 2007; Lindgren et al. 2010; Bell et al. 2011), feeding (Collin and Janis 1997; Rayfield et al. 2007; Goswami et al. 2011), reproduction (Cheng et al. 2004; Botha-Brink and Modesto 2007) and defence (Chirat et al. 2013). Many of these biological convergences began to be understood as adaptations within tightly constrained physical laws, nature 'engineering' the same optimal solutions in response to the same evolutionary problems (Raup and Michelson 1965; Schindel 1990; Pierce et al. 2008).

In 1989 Stephen J. Gould published his influential work 'Wonderful Life' which synthesised many of the ideas in macroevolutionary and palaeontological theory which had emerged since Simpson (Gould 1989). He argued that studies of the fossil record showed that patterns of diversity through time are dominated by significant environmental shifts and catastrophic events, with little obvious reason behind which groups survive and which don't (Jablonski 2005). As subsequent evolution seemed to be strongly dependent on the nature of the survivors, whether any given clade persists seemed to be determined by pure chance. Gould's view was heavily informed by the earliest diversification of complex animals, the so-called 'Cambrian Explosion' some 541 million years ago. In the 1920s, discoveries from Burgess Shale of Canada provided the first evidence of many of the major animal groups including molluscs, arthropods and vertebrates (Yochelson 1996). Later reinterpretation in the 1970s revealed that many of these early animals in fact did not fit into established groups, showing forms which were either almost completely alien or a bizarre mosaic of traits across the animal tree (Whittington 1975; Conway Morris 1977; Whittington and Briggs 1985). The range of forms was staggering, probably greater than at any other time in earth's history, with many of the stranger bodyplans disappearing from the record soon after (Briggs et al. 1992; Fortey et al. 1996). Gould wondered how our knowledge of evolutionary process could possibly predict such a varied range of wildly different solutions. He emphasised the importance of contingency in evolution most succinctly with the metaphor of 'replaying life's tape'. In his view, re-running the history of life from the beginning would produce vastly different outcomes, evolution being a stochastic phenomenon where minute differences in starting conditions amplify exponentially to produce radically different outcomes. This emerging picture of an evolutionary process in which each

change was influenced by those that occurred prior, punctuated by extremely strong selection seemingly at random as the environment changes resulted in a view of evolution as a highly chaotic process, impossible to predict without unfeasibly precise knowledge of starting conditions and the exact sequence of perturbations.

The Gouldian model of evolution was far from universally accepted, with some scientists arguing that physical and ecological pressures were likely to limit evolution to a finite number of possible outcomes in some circumstances. Most notably, Simon Conway Morris strongly advocated convergent evolution as an indicator of macroevolutionary process. In several publications during the 1990s and early 2000's (Conway Morris 1998; Conway Morris 2004; Conway Morris 2006) he argued that the staggering number of instances of convergent evolution showed that evolution produced a finite number of adaptations in the majority of circumstances, with constraint and iteration of structures being the rule, rather than the exception. The years following brought renewed interest in studying convergent evolution as a macroevolutionary phenomenon, with many more compelling examples being presented and much discussion of how to recognise it in extant organisms and the fossil record (Conway Morris 2010).

1.1.5 Summary

Much of the appeal of evolutionary theory, ever since the work of Darwin lies in its ability to explain widespread biological patterns. While studying the origin of evolutionary novelty has been the main focus of evolutionary theory, mechanisms with which to explain the abundance of phenotypic similarities are also required. It was originally supposed that these similarities were due to common ancestry, however, the more quantitative approaches of the modern synthesis revealed that many of these similar traits were shared by distantly related taxa. Whilst many of these traits were interpreted as adaptations to similar environments or selective pressures, developments in our understanding of molecular evolution revealed that these evolutionary convergences were more common that first realised and that the Darwinian emphasis on selective pressures did not necessarily provide the best explanation for these patterns. A renewed interest in macroevolutionary patterns and evolutionary palaeontology highlighted the ubiquitous recurrence of many morphological traits, prompting authors like Conway Morris to argue for the importance of convergence as a general evolutionary principle.

1.2. Convergent Evolution

1.2.1 Defining & Characterising Convergent Evolution

Despite the patterns and processes of convergent evolution being a part of evolutionary theory since its origin, definitions of what exactly constitutes convergence vary greatly. This is partly due to convergent evolution having been used within the context of a

staggeringly diverse range of systems and disciplines, from molecular evolution (Zuckerkandl and Pauling 1965a; Bork et al. 1993; Mattevi et al. 1996) to the behavioural sciences (Emery and Clayton 2004; Blackledge and Gillespie 2004). Stayton in his 2015 review of definitions and measures of convergent evolution stated that many biologists view convergent evolution as self-evident and therefore requiring neither precise definition or specialised means of analysis (Stayton 2015). The absence of agreed upon, clearly defined definitions has been recognised as a major hurdle impeding progress in the field (Doolittle 1994; Stayton 2015)

1.2.1.1 General Agreement

There are some aspects of convergence that are almost always agreed upon. Almost all definitions describe a pattern in which similar characteristics (phenotypes or genotypes) evolve independently in multiple lineages (Losos 2011a; Wake et al. 2011; McGhee 2011; Collar et al. 2014; Starr et al. 2015). In practical terms, authors use phraseology like “different groups” (Simpson 1949), “no common heritage” (Mayr 1970) or “unrelated organisms” (Travis and Reznick 2009) to signify that the organisms in question are distantly related enough to make it highly unlikely that the shared trait in question was inherited from a common ancestor or evolved due to chance. Similarity retained from a common ancestor is not regarded as convergence (Conover and Schultz 1995), although in practice some measures of convergence, such as homoplasy on phylogenetic trees (Wake et al. 2011) or measures of phenotypic and phylogenetic distance (Stayton 2008; Muschick et al. 2012) do not make this distinction.

1.2.1.2 Pattern & Process Based Definitions

Although independently evolved similarity is a common feature of all definitions of convergent evolution, there is a general confusion of pattern and process based definitions (Stayton 2015). Pattern-based definitions are process-neutral, making no assumptions about why the phenotypes have independently evolved. Process-based definitions attribute the phenomenon of convergence to a specific evolutionary cause. The difference is most often apparent when considering whether convergent evolution is explicitly adaptive, as some definitions state (Futuyma 1998; Freeman 1998; Pagel 2002; Freeman and Herron 2007; Hine 2008; Russell et al. 2008; Travis and Reznick 2009). This is clearly conceptually different from using instances of convergence (defined using process-neutral terms) as evidence for evolutionary adaptation, as other workers have done (Blackburn 1992; Harmon et al. 2005; Losos 2011a). Which approach one uses has a significant effect on how one goes about testing evolutionary hypotheses. Process-based definitions (adaptive or otherwise) require robust proof that that process is operating on the organisms in question before patterns of similarity can be identified as convergence. Pattern-based definitions are often the exact opposite, they use manifest

patterns of convergence as evidence for underlying evolutionary processes such as adaptation.

1.2.1.3 Parallelism & Convergence

The status of convergent evolution as a pattern-based or process-based phenomenon has indirectly led to confusion and contradiction in other areas, principally the distinction between convergent evolution and parallelism. Typically, convergence refers to independently evolved features which are superficially similar but arise from different developmental pathways or are structurally different (Futuyma 1998), while parallelism refers to the same trait evolving repeatedly from the same developmental pathway (Zhang and Kumar 1997; Colosimo et al. 2004). In practice it can be difficult to distinguish whether two organisms truly share the same developmental pathway, partly because of the difficulty of identifying the correct pathway and partly because there is no clear definition as to what constitutes sufficient genetic or developmental similarity (Powell 2007; Wake et al. 2011). While purely topological criteria for convergence and parallelism have been developed to attempt to deal with these issues, these definitions can conflict with the more traditional developmental classifications in some cases (Pearce 2011). Confusingly, some authors reserve the term 'convergence' for similarity produced through adaptation (consistent with some process-based definitions) but use parallelism to refer to similar patterns produced by developmental constraints (Yoon and Baum 2004). This is problematic when both constraint and selection can theoretically give rise to identical patterns. The difficulty of precisely delimiting convergence and parallelism has led some authors to question whether a distinction can or should be made at all (Arendt and Reznick 2008).

Similar 'convergent patterns' have been shown to result from adaptation (Winemiller et al. 1995; Bernal et al. 2001; Meinzer 2003), constraint (Wake 1991; Jaekel and Wake 2007) or a combination of both (Donoghue 2005; Losos 2011a; Wake et al. 2011). Convergent patterns can even emerge purely through neutral processes (Stayton 2008). Any process-based definition of convergence must, therefore, explicitly test for the evolutionary mechanism by which convergent evolution is theorised to occur. In practice, many who have used process-based definitions fail to test whether the patterns they observe could occur by processes other than the one they hypothesise.

1.2.2 Types Of Convergence

Many previous studies have leaned very heavily on identifying and discussing specific examples of convergence , often with the aim of convincing the reader of the remarkable or pervasive nature of such examples (Conway Morris 2010). Examples that the authors feel are the most 'self-evident' or require the least explanation or investigation are often

preferred as being ‘more persuasive’. Many of the examples that have garnered the most attention are traits which are seen to be particularly complex, specialised or show numerous repeats (e.g. as part of adaptive radiations). Some general types of convergence have been frequently discussed in the literature, although these definitions are often not mutually exclusive. A brief discussion with some illustrative examples follows below.

1.2.2.1 Functional Convergence

Many of the earliest discussed examples of convergent evolution in the literature were general forms or features with similar functions, interpreted as adaptations to specific environments. The independent acquisition of similar kinds of styles of locomotion or appendages are classic examples. Powered flight, for instance, has been acquired independently in insects, birds, pterosaurs and bats. While insect wings are clearly structurally very different from their vertebrate counterparts, the convergent evolution of flight in vertebrates shares several striking similarities. All three groups show the elongation of limb bones to form a support for an aerodynamic surface along with complementary changes in musculature and the rest of the skeleton, although which elements are used and their precise structural function differ (Lull 1906). It appears that achieving flight also involved a decoupling of function between the fore and hind limb in each case, probably convergently (Bell et al. 2011).

Another example of striking convergence in function are the limbs and body forms of active swimmers among vertebrates. Sharks, tuna, ichthyosaurs and dolphins have all convergently evolved similar thunniform body-plans from highly morphologically disparate ancestors. All groups show a high degree of similarity in both caudal and dorsal fin shape (Lingham-Soliar 2005c), with clear hydrodynamic advantages (Lingham-Soliar 2005a; Lingham-Soliar 2005b). Furthermore, there is taphonomic evidence that some ichthyosaurs convergently evolved collagen fibres to stiffen the integument of control surfaces (Lingham-Soliar and Plodowski 2007). Similar structures are seen in living thunniform sharks and are interpreted as an adaptation to cope with torsional stresses during swimming (Lingham-Soliar 2005b).

Examples of functional convergence are also plentiful in other biological systems . Sensory systems often evolve convergent similarities. One often discussed example is the independent evolution of eyes in such distantly related groups as arthropods, molluscs (Barber and Wright 1969), chordates, cnidarians (Piatigorsky and Kozmik 2004) and annelids (Bok et al. 2016). Whilst eyes often perform very similar functions and utilise a relatively restricted number of opsins, the structures and methods used to capture an image are often very different (Land and Fernald 1992). Another often discussed example of functional convergence is the independent evolution of

echolocation in several disparate groups, sometimes to a highly specialised degree, as in microbats, cetaceans and birds (Brinkløv et al. 2013). Several studies have suggested that this general functional convergence might be underpinned by more fundamental genetic similarities (Parker et al. 2013). Recent studies suggest that similarities in other traits among echolocating taxa do not deviate significantly from random, suggesting a different genetic basis in each case. Functional convergence is often documented in integrated structures with a common mechanical purpose (e.g. feeding structures). Specialised feeding structures especially, such as the proboscises of nectar feeding and blood sucking insects, durophagous (shell-crushing) jaw morphologies in fish (Grubich 2003) and carnivorous adaptations in plants (Albert et al. 1992) appear to have evolved convergently many times. In plants, complex traits such as floral structures evolved functional adaptations independently, possibly in response to strong selection pressures from pollinators. Ontogenetic colour changes in turgid flowers are common and appear in at least 77 families across the angiosperm tree (Weiss 1995). The degree of colour change is broadly correlated with the pollinator type, despite 7 different physiological mechanisms of producing the change.

1.2.2.2 Structural Convergence

In some cases, the shared similarity runs deeper than similarities of function or shape. Traits can also show varying degrees of structural convergence, as the shared arrangement and composition of the components within the structures themselves is also derived independently, rather than inherited from a common ancestor.

One of the most commonly cited and compelling examples of convergent evolution occurs in the camera eyes of cephalopod molluscs and vertebrates. In both cases, light is collected using an aperture and focused using manipulation of an optical lens onto a retina at the back of the eye, stimulating photoreceptors which relay the signal to the central nervous system via an optic nerve. Each component of this system evolved entirely independently (Fernald 2000). There are differences however. Derived vertebrates (birds and mammals) focus the lens by changing its shape, while cephalopods change the position of the lens forwards and back in a similar manner to teleost fish (Sivak 1982). Eye lens proteins are also different in each case, although some of the developmental genes (famously Pax-6) appear to have evolved early in animal evolution and were recruited repeatedly (Fernald 2006). It appears, therefore, that while the degree of structural convergence is dependent on the level of organisation at which one looks, there is often deeper, highly conserved homology at the molecular level (i.e. in the genetic mechanisms of development).

In some cases, however, structural similarities occur even at the molecular level. Lignin and secondary cell walls (traits thought unique to vascular plants) have been reported in

a coralline red alga (Martone et al. 2009), despite around 1 billion years of evolutionary history separating the two groups. Cysteine rich proteins which confer mechanical resistance in hair have also been found in feathers. Lizard and avian epidermal differentiation complex proteins (EDCPs) are likely homologous with each other, but non-homologous with mammalian keratin-associated proteins (KrtAPs). Another example of these kinds of close structural similarities can be found in the microstructure of gastropod shells. Analysis of lamellar structure and phylogeny in thiarid gastropod taxa of Lake Tanganyika revealed that there had likely been at least two independent origins of three crossed-lamellar layers and two origins of four crossed-lamellar layers in the group.

Although many examples of functional convergence also involve a degree of structural convergence, this is not always the case. Opposable 'thumbs' have evolved independently in primates, the giant panda and the red panda. However, while primates have co-opted the first digit to evolve opposability (Napier 1962), pandas have evolved a 'false thumb' from the radial sesamoid of the wrist (Salesa et al. 2006; Antón et al. 2006). While functionally convergent, these two types of 'thumb' are complete analogous structures. Fruit structures in flowering plants represent another example. While functionally similar, fruits are derived from a variety of floral tissues. For example, the fruit of tomatoes is derived only from ovary tissue, apples from hypanthium and strawberries from the tissues of the receptacle via different genes with similar regulatory functions (Ireland et al. 2013).

1.2.2.3 Mechanistic Convergence

In many cases, traits which are convergent in some functional or structural aspect owe their similarity to highly conserved homologies at the genetic level, which may manifest at the phenotypic level in separate distinct events (Shubin et al. 2009). These highly conserved genetic mechanisms inherited from a common ancestor are classically termed 'deep homologies', to distinguish them from more traditionally defined homologies based on the structure, arrangement and composition of phenotypic traits. In the most notable and extreme cases of convergence, structural similarities are not the result of 'deep homology' but are derived from the independent acquisition of the same or highly similar developmental pathways. These kinds of convergences are, in practice, extremely difficult to identify as they require a detailed knowledge of the biochemical and physiological processes that gave rise to the structure and because it is often difficult to rule out parallel evolution from shared developmental precursors. There are, therefore, few likely candidates, all of which are somewhat contentious. Some of the best known of these are discussed below.

Mimicry, specifically in the wing patterns of butterflies, is often discussed as a striking and pervasive example of convergent evolution (Punnett 1915). Two types of mimics are

common throughout the Nymphalidae, Batesian mimics and Műllerian mimics. While Batesian mimics copy the form of an unpalatable species despite being palatable (Pfennig et al. 2001), Műllerian are unpalatable forms that have converged on the same form as a warning signal to predators (Mallet 1999). Genetic studies of *Heliconius* have revealed multiple convergent mimics, even within the same species (Brower 1994). Mutations in a single gene (*optix*) have been linked to the evolution of red warning colour patterns independently in at least 4 species of *Heliconius* (Reed et al. 2011) strongly implying the mechanisms responsible have also evolved convergently. A variety of other pigmentation patterns are also thought to have evolved convergently via similar mechanisms in a number of other groups, such as White Sands lizards and Drosophila (Kronforst et al. 2012). In cave fish, the convergent evolution of albinism is linked to deletions in the gene *Oca2*. The deletions have occurred in different places in the same gene in each case and so almost certainly occurred independently (Protas et al. 2006)

Lepidopteran eyespots have also evolved convergently in different groups. While eyespot formation utilises several different developmental mechanisms (Shirai et al. 2012), similar focal marker genes are found in the eyespots of nymphalid butterflies and saturniid moths (Monteiro et al. 2006; Oliver et al. 2012). The mechanisms in these two groups are very likely to have evolved convergently as the eyespots are situated in non-homologous areas of the wing in each case (Monteiro 2008). Similar pigmented spots have also evolved independently in different fish groups (Neudecker 1989; Beeching 1993). Remarkably, the formation and repair of colour spots in fish species has been shown to be in many ways identical to that of Lepidopteran eyespots, suggesting that serial induction mechanisms of eyespot formation have evolved independently in two extremely distantly related groups (Ohno and Otaki 2012).

One of the most famous examples of mechanistic convergence is the independent evolution of C_4 photosynthesis, in which CO_2 is concentrated through various pathways around the enzyme Ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) in order to prevent wasteful fixation of oxygen in photorespiration (Hatch 1987). C_4 photosynthesis has likely evolved independently in plants at least 45 times (Sage 2004). In at least some cases, the same sets of genes involved in C_4 pathways also appear to have evolved convergently. In grasses (Poaceae), C_4 photosynthesis involving the enzyme PEPC were found to have evolved 8 times independently, involving the convergent evolution of 21 amino acids to be highly similar or identical in each case (Christin et al. 2007). The same phenomenon has also been documented in sedges (Cyperaceae) (Besnard et al. 2009), with large portions of the *rbc*L gene evolving independently 23 times across the two groups (Christin et al. 2008).

1.2.3 Convergent Adaptive Radiations

While convergent evolution can occur in isolation, it can also occur in parallel series or sets of traits. In particular, convergent evolution has often been associated with adaptive radiations where groups develop new forms as they rapidly diversify into new niches (Simpson 1953; Schluter 2000). Some well-known examples of this phenomenon, in a range of groups and at a range of scales, are discussed below.

1.2.3.1 Island Scale

Many of the classic examples of adaptive radiations concern clades which diversified on islands. These geographical microcosms allow detailed study of the dynamics of speciation and niche occupation, often in clades with relatively short (and therefore unobscured) evolutionary histories. In the Greater Antilles, lizard species in the genus *Anolis* have convergently evolved highly similar twig, trunk-ground, trunk-crown and crown giant ecomorphs on all 4 islands of the Greater Antilles (Losos 1992). Lesser Antilles anoles also show some of these morphs, but also some unique morphs, with trunk-crown morphs being the most common and likely the ancestral form (Losos and Queiroz 1997). Quantitative analysis has shown that species within each ectomorph of the Greater Antilles also show convergent patterns of body size, body shape, head shape, digit lamella number and sexual size dimorphism (Harmon et al. 2005). Similar patterns of convergent ectomorphs have also evolved in Hawaiian spiders, which show a number of web type 'ethomorphs' shared across islands (Blackledge and Gillespie 2004). *Tetragnatha* spiders on Hawaii have evolved 4 different morphs of 'spiny leg' forms which have also been shown to have evolved convergently on different islands (Gillespie 2004).

Isolated geographical replicates also exist in systems besides 'traditional' islands. Cichlids are a highly speciose group of fish which have diversified rapidly in African Rift Valley lakes (Kocher 2004). In many cases, remarkably similar phenotypes have evolved completely independently. DNA analysis of cichlid species in Lake Malawi and Lake Tanganyika confirmed that the species populations of the two lakes have two completely separate origins (Kocher et al. 1993), despite striking convergences in ecology (Ruber and Adams 2001) and body-form (Muschick et al. 2012). This kind of repeated convergent evolution may also have occurred in a number of other cases, for example in 3-spine sticklebacks in glacial lakes (Schluter and Nagel 1995).

1.2.3.2 Continent Scale

Convergent radiations have also been observed across continents. Mammals have convergently evolved a very similar range of body-forms in their two major radiations; the placentals in North America, Africa and Europe and the marsupials of South America

and Australasia (Springer et al. 1997). In particular, skull shapes seem to have independently converged on similar structural properties and morphologies in the two groups, including insectivorous, omnivorous and carnivorous forms (Wroe and Milne 2007; Goswami et al. 2011). Convergence towards highly specialised morphologies also occurred, with fossorial mole like forms (Nevo 1979), ant and termite eaters (McNab 1984), gliding arboreal taxa (Jackson 2000) and specialised hypercarnivores (Wroe et al. 2013) evolving in each group.

Several groups of anurans also show convergent evolution in clades diversifying on separate land masses. Ranid frogs show a number of convergent trends towards similar forms in Madagascar and Asia including burrowing toad-like forms, keratinized teeth in tadpoles, complete metamorphosis in the egg in some arboreal forms, semi-terrestrial larvae in rock dwelling forms and fanged species (Bossuyt and Milinkovitch 2000). Similar patterns are mirrored across continents in frogs as a whole, with morphotypes associated with similar ecologies (burrowing, semi-aquatic, terrestrial, arboreal) in all major clades (Moen et al. 2013). Such patterns are not limited to animals. In flowering plants, adaptations to different pollinators including beetles (Bernhardt 2000), bats (Knudsen and Tollsten 1995) and arboreal mammals (Rourke and Wiens 1977) have appeared independently in several Old and New World families.

1.2.4 Convergence At Different Organisational Levels

Although demonstrating the diverse and ubiquitous nature of convergent evolution, the traditional terminology used to categorise convergence presents difficulties. Distinctions of parallel and convergent evolution become problematic when there are degrees of developmental similarity and aspects of genetic architecture common to all groups (Arendt and Reznick 2008; Scotland 2011; Pearce 2011; Wake et al. 2011). The line between functional and structural convergence becomes blurred when some structural similarities are almost always inherent to function. Most definitions of structural convergence are at least somewhat ambiguous, as structural differences at some level or in some aspect are likely responsible for the trait being recognised as convergent in the first place. Perhaps the most precisely delimited category of convergence is mechanistic or molecular convergence, but in this case it can be even more difficult to make any distinction between parallelism and ‘true’ convergence.

Convergent evolution can manifest at all scales and this is to some extent tied up into current categorisations, even when such links are not explicit. For example, many examples of functional convergence are properties of whole organisms or organ systems. The most extreme example of this is the recognition of the convergent evolution of behaviours and cogitative processes, such as the evolution of metatool use in corvids and primates (Emery and Clayton 2004; Taylor et al. 2007) or eusociality evolving around

11 times in insects (Woodard et al. 2011). Many of the examples of functional convergence discussed in this chapter operate across the whole phenotype (thunniform body-plans, convergent forms of marsupial and placental mammals, echolocation) or are manifest in the generalities of a complex trait (e.g. wings, caudal fins, jaws). Most examples of structural convergence mirror these broad similarities at lower organisational levels. The camera eyes of squid and vertebrates are convergent at the level of the whole organ, but also show a high degree of similarity within the structure and arrangement of tissue and cell types (Land and Fernald 1992). Examples of convergence at a lower level of organisation include similarities in the electric organs of fish (Zakon et al. 2006) and structurally producing collagen arrays in mammals (Prum 2004). At the lowest level of organisation convergent evolution creates similarity at the cellular level (e.g. eyespots and pigmentation patterns) or even at the molecular level (Roux et al. 1998). Classifying convergence based on the level of organismal organisation at which it occurs explicitly delimits where the convergent patterns exist and precisely which forms or aspects of form are hypothesised to be 'the same', without conflating that pattern with process or evolutionary mechanism.

1.2.5 Summary

Despite frequent discussion, the concept of convergent evolution is surprisingly poorly defined. A key distinction is whether convergent evolution is defined purely on the basis of pattern or whether the term also refers to a particular evolutionary process (most commonly adaptation). For the purposes of studying convergent evolution and its effects in a holistic and quantitative manner pattern based definitions are advantageous as they make fewer assumptions and are more amenable to robust tests of evolutionary hypotheses (Stayton 2015). Although several types of convergent evolution are recognised, the existing literature often utilises overlapping definitions and is often ambiguous in separating pattern and process. Classifying convergence based on the degree of organisation or complexity of the structure it is manifest in might provide a means of untangling patterns and investigating underlying processes.

1.3. Quantifying Convergence

Given the variety of definitions and types of convergence, it is not surprising that a wide range of techniques have been proposed to investigate convergent evolution empirically. Each method has a number of advantages and shortcomings, with no single method being perfectly suited to all cases. A brief summary of different methods follows.

1.3.1 Quantifying Degree Of Similarity & Difference

While discrete character data can be used in studies of convergence most attempts to quantify phenotypic variation have focused on continuous measurements. What follows

is a summary of methods of morphometric analysis to place the various subsequent methods in context. For a more detailed account of different types of morphospace and the processes of deriving them, please refer to the introduction of Chapter 2.

A number of approaches to quantifying variation in form (collectively known as morphometric approaches) exist (Adams et al. 2013). In the simplest methods of morphometric analysis a few linear measurements or simple indices are used to define a space which represents the range of form shown by taxa (Streissl and Hödl 2002; Lingham-Soliar 2005c). This space is an empirical morphospace, in which taxa are represented by points in the space and the distances and relative positions between points are a reflection of their differences in form (Huntley et al. 2006). In practice, morphospaces are often highly multidimensional, as each measured variable of form corresponds to an axis of variation in the morphospace. Multivariate ordination techniques such as principal components analysis (Abdi and Williams 2010) or principle co-ordinates analysis (Gower 2005) are often used to reduce the number of axes of variation for visual representation and further analysis. In many recent studies nets of homologous landmark co-ordinates taken from morphological structures (MacLeod 2001) or semi-landmark points on outlines (Perez et al. 2006) are used to quantify variation in form, but theoretically almost any variable can be used to define a morphospace. If evolutionary relationships between the taxa are known, the 2D phylogeny can be projected into the multdimentional morphospace to create a 'phylomorphospace' (Sidlauskas 2008).

1.3.2 Frequency Based Measures

The most common assessments of the effect of convergent evolution are simply to count the number of times convergent evolution of a particular type takes place. Studies by authors such as Conway Morris (Conway Morris 2004) and McGhee (McGhee 2011) essentially employed this method in a qualitative way to highlight the pervasive nature of convergence. A slightly more empirical method is to count the number of times species are more similar to a target species then that target's closest relative (Winemiller 1991). Alternatively, one can count the number of species that are not most phenotypically similar to their closest relative (Stayton 2008). The problem with count approaches is that they only identify convergence in taxa that are closest neighbours in phenotypic space. A measure based on phenotypic similarity in the morphospace was provided by Stayton in his C_5 metric (Stayton 2015). A region of interest is defined within a phylomorphospace, either a priori from mechanical or theoretical considerations or by defining an area from an existing set of species using approaches like minimum convex hull or confidence ellipsoids. This region represents the zone of phenotypic similarity in the morphospace that is convergent. C_5 is defined simply as the number of times taxa

are inferred by the phylogeny to cross into the region of interest from the outside. C_5 can be scaled relative to the total number of taxa or over a given interval of time, by calculating phylomorphospaces at successive time slices. The main problem with this approach is that it requires some criterion with which to define the region of interest and can only be used for taxa with forms similar enough to quantify with the same variables.

1.3.3 Distance Based Measures

Another of Stayton's measures of convergence operates on the principle that convergence will lead to greater similarity between descendants than between ancestors defined thus:

$C_1 = 1– (D_{tip}/D_{max})$

Where D_{tip} is the phenotypic difference between tip taxa in the morphospace (e.g. Euclidean or Procrustes distance) and D_{max} is the maximum distance between any two taxa in that lineage. C_1 ranges from 0 to 1 and represents the proportion of 'phenotypic distance' between two taxa in a lineage which has subsequently 'closed'. A number of modifications of this metric exist. For example, the magnitude of change can be taken into account when only comparing within datasets:

$C_2 = D_{tip}/D_{max}$

C_2 can then be divided by the total branch length in the morphospace of that lineage or the total branch length to the root of the clade, to scale phenotypic difference relative to the total amount of phenotypic change in that lineage or from the root respectively. The main problem with this approach is that it is heavily reliant on ancestral state reconstructions to quantify variation between taxa in a lineage. Ancestral state reconstructions are often problematic in many groups, with error increasing further away from the tips (Cunningham et al. 1998; Losos 2011b; Duchêne and Lanfear 2015). In particular, ancestral state reconstructions are often constrained within the bounds of variation seen in extant taxa (Stayton 2015). This will tend to inflate Type II error and lead to underestimates of these kinds of distance-based measures.

1.3.4 Clustering Methods

Some measures of convergence attempt to quantify degree of similarity through some metric of clustering. The Multidimentional Convergence Index (MCI) (Stayton 2006) is the ratio of the total disparity of sister taxa to the total disparity of all convergent taxa. If the MCI is greater than 1 then the convergent taxa are more clustered in the morphospace than their sister taxa. The 'Wheatsheaf' Index (Arbuckle et al. 2014) is a modification of this concept which measures convergence as the ratio of average pairwise distances between all taxa in the dataset to the average pairwise distances

between all hypothesised convergent taxa. Both the MCI and 'Wheatsheaf' Index are not true measures of convergence however, as both fail to distinguish acquired similarity from phenotypic stasis (Stayton 2015).

1.3.5 Phylogenetic Distance

Several measures of convergence have been proposed based on the expectation that similarity should be greater for more closely related taxa. These measures use some variant of the ratio of phylogenetic distance to phenotypic distance. One attempt to quantify the degree of convergence in species of cichlid fish (Muschick et al. 2012) calculated the morphological distance between all possible species pairs as Euclidean distances from a regression of shape against centroid size for all individuals (pooled within species). The expected effect of phylogenetic distance on morphological differences was then assessed using Brownian motion and Ornstein-Uhlenbeck models before calculating Euclidean distances from these simulations of neutral trait evolution. The statistical significance of differences in pointwise mean Euclidean distances of simulations was then evaluated using bootstrap randomisations. Another method by Stayton instead takes the ratio of the patristic distance to the phenetic distance for all possible pairs of taxa and averages it across the tree, with the idea that highly convergent taxa will have a very short phenetic distance relative to their patristic distance (Stayton 2008). As both distances depend on the tree length and traits being used, values were divided by the maximum observed in each dataset to make them proportional. While both of these measures are useful in assessing the degree of 'partial' convergences, they again fail to separate convergent evolution from phenotypic stasis.

1.3.6 Process Based Measures

The SURFACE model (Ingram and Mahler 2013) infers a number of 'selective regimes' by fitting a number of increasingly complex Ornstein-Uhlenbeck models to a phylogenetic tree, using the Akaike Information Criterion to select the best one. The number of convergences is then inferred from the number of lineages sharing a selective regime with another lineage. The main flaw with this approach as a measure of convergence is that independent shifts towards the same selective regime are the only criterion which defines convergence and the selective regimes themselves are inferred from the model. While this operates perfectly well as a conceptual hypothesis to then test with biological observations it does not by itself constitute substantial evidence of convergent evolution.

1.3.7 Summary

Although many measures of convergence have been proposed, most fail to capture some aspect of what makes the phenomenon of interest to biologists. Process-based methods, such as SURFACE, do not directly identify or quantify convergence but instead

use probabilistic models to infer where convergence has possibly taken place. Frequency based measures commonly can only identify instances of convergence between taxa that are closest to each other in phenotypic space and do not measure degree of convergence in any sense. Both clustering measures and methods based on phylogenetic distance fail to distinguish between convergence and phenotypic stasis and so do not really quantify convergence as it is commonly understood. While phylomorphometric methods provide a more robust quantification, their dependence on ancestral state reconstructions, resolved phylogenies and a defined morphospace limits their useful application to groups with recent origins or an exceptional fossil record. Even in these cases, the methods assume that related taxa represent discrete evolutionary lineages. This kind of evolutionary series is incredibly unlikely to be found in the fossil record. It also presents difficulties with regard to the interpretation of convergence, as it can be unclear what 'convergence' in a multivariate ordinal space represents. These limitations make phylomorphic methods best suited to case studies of groups with largely homologous, well studied anatomies and well characterised evolutionary histories, but of limited use in studies of how convergent patterns manifest over long macroevolutionary timeframes.

1.4 The Macroevolutionary Impact of Convergence

How does convergent evolution manifest in macroevolutionary patterns and what does this tell us about the process by which evolution operates over long timescales? Convergent evolution is likely to have significant consequences for the evolution of the range of form (disparity), the recursion of traits (homoplasy) and the evolvability of organisms (diversification).

1.4.1 Diversity Through Time

There seems to be a general trend towards greater diversity through geological time, as evident from the marine fossil record (Sepkoski et al. 1981; Sepkoski 1997) and calcareous nannoplankton (Bown et al. 2004), as well as within groups like crown birds (Jetz et al. 2012) and mammals (Bininda-Emonds et al. 2007). However, the quality of the fossil record also improves through time (the 'pull of the recent'). Correcting for rock record and sampling biases generally can change diversity trends significantly, but in many cases there is still a trend towards increasing diversity through time (Benton 2009; Sahnay and Benton 2017). Convergent evolution is suggestive of a restricted capacity to evolve entirely novel traits, which could logically impact the evolution of derived characters (autapomorphies in cladistics) and hence diversification. Environmental factors such as climate and competition, or intrinsic developmental limitations could constrain the evolution of morphological traits by strongly selecting against ones with low

fitness and promoting a restricted range of 'evolutionarily viable solutions' (Arnold 1992). This is best illustrated with the concept of 'key innovations', entirely novel traits which allow taxa to escape these environmental limits and facilitate explosive diversification once they arise in a clade (Vamosi and Vamosi 2010; Etienne and Haegeman 2012; Bhullar et al. 2015). In practice, as environmental factors such as resource availability and climate change also have a significant direct impact on diversity (Stroud and Losos 2016) this hypothesis would only be robustly supported if it was demonstrated that low diversity clades tend to exhibit a restricted number of convergent traits linked to particular environments or developmental constraints. The prevalence of convergence in adaptive radiations (Harmon et al. 2005; Muschick et al. 2012) suggests selective pressures to evolve convergent forms likely promote diversification, by driving morphological and ecological specialisation into niches.

1.4.2 Morphological Disparity

One of the main areas of study in macroevolutionary biology is how the range of forms organisms have evolved changes through geological time. Although conceptually linked, variation in organism form is distinct from diversity measures and is referred to as 'morphological disparity', 'morphological variety' or simply 'disparity' (Wills et al. 1994; Foote 1996a; Fortey et al. 1997). As the diversity of taxa in a group is, at least in a theoretical sense, a representation of the number of different forms, the simplest view is that as diversity increases, disparity increases accordingly. Several studies of patterns of overall disparity through time have shown that this is not the case and that patterns of disparity and diversity are nearly always decoupled (Foote 1991a; Fortey et al. 1996). If convergent evolution is a ubiquitous macroevolutionary phenomenon, one of its hypothesised effects would be to limit the disparity of clades. Patterns of overall disparity through time do indeed appear to be limited, at least in animal groups. Analysis (**Fig. 1.1**) of a sample of 98 metazoan clades showed that most clades reach or approach maximum disparity early in their evolutionary history (Hughes et al. 2013). While this is consistent with the hypothesis that convergent evolution tends to restrict the range of form that evolve over macroevolutionary time, similar trends have not yet been identified in other groups of organisms. There are a number of mechanisms that could create such a pattern, such as a slowdown in the rate at which new characters evolve (Wagner 2000), restrictions on available ecospace (Benson et al. 2014), or genetic, developmental or functional constraint (Niklas and Kerchner 1984; Collin and Janis 1997; Losos 2011a).

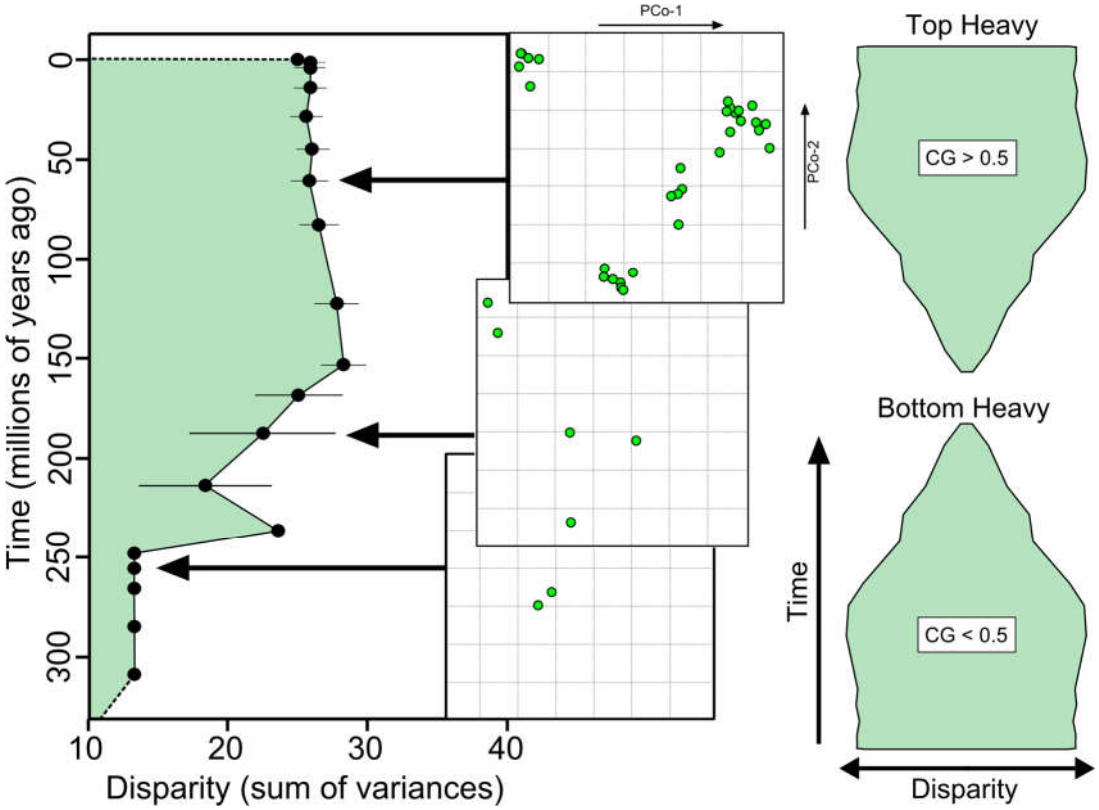

Fig. 1.1 Generating a disparity profile, following the approach of Hughes et al. 2013. (A) Disparity of conifers (Pinales) measured as the sum of variances on all principal coordinates for each time bin. Values are the mean of 1,000 bootstrap replicates ± SE. (B) Distribution of taxa on the first two principal coordinates of the empirical morphospace at three of the time bins. Green points represent taxa present in that bin, grey points indicate taxa present in other bins. (C) Stylized illustrations of significantly top-heavy (Upper) and bottom-heavy (Lower) disparity profiles.

1.4.3 Homoplasy

Convergent evolution also impacts how characters evolve on phylogenetic trees. Specifically, convergence contributes to the phenomenon known as homoplasy, in which characters hypothesised to be identical are reconstructed as having multiple origins on an evolutionary tree (Sanderson and Donoghue 1989; Powell 2007). Some authors have even gone as far as to use metrics formulated to measure homoplasy as a means of quantifying convergence (Sanderson and Hufford 1996; Ackerly and Donoghue 1998). However, homoplasy is not purely a representation of convergent evolution as typically understood, as parallelism and reversals also contribute to homoplasy. As discussed previously, it is controversial whether there is a fundamental distinction between parallelism and 'true' convergence (Arendt and Reznick 2008; Scotland 2011). In a purely phylogenetic sense, the two patterns are defined solely based on phylogenetic distance, which is a continuum rather than discretely limited, making any distinction arbitrary. Reversals can be distinguished however, as they signify the reappearance of an ancestral state and the loss of a novel character (apomorphy). This is distinct from convergence, which is the independent acquisition of a novel character (apomorphy) in two or more lineages. The advantage of quantifying homoplasy in studies of convergence are it directly relates to the inference of evolutionary relationships, it is easily measured using existing morphological datasets, general patterns can be directly compared across clades and it is relatively easy to identify exactly which traits are arising independently. These properties make measures of homoplasy particularly well suited to the kinds of analyses of general patterns that are the aim of this thesis.

1.4.4 Summary

Convergent evolution is expected to impact macroevolutionary patterns in a number of ways, primarily through limiting the variation of form (disparity) and the recurrent evolution of traits (homoplasy). Although convergent evolution probably also impacts the evolution of diversity, the nature of this effect is unclear. Developing a more complete understanding of the importance of convergent evolution requires these macroevolutionary patterns and the interactions between them to be quantified more comprehensively to formulate and test hypotheses regarding evolutionary constraint.

1.5 Thesis Aims

The goal of this thesis is to investigate the importance of convergent evolution in shaping macroevolutionary patterns, focusing on identifying the general trends across a wide range of clades of organisms. Specifically, the thesis focuses on the hypothesis that convergence reflects evolutionary constraint, testing for the ubiquity of such patterns and where and why such constraints might be imposed. The identification and characterisation of these patterns will help to inform whether 'laws of evolution' do exist and to what extent evolutionary outcomes are predictable.

i) To investigate the evidence for general constraints in macroevolution by quantifying patterns of morphological disparity in organisms more widely, focusing on similarities and differences between disparity patterns in plants and animals and the extent to which diversity and disparity patterns correlate.

ii) To test whether macroevolutionary patterns of overall morphological disparity can be explained by simple physical limits on the range of forms traits can exhibit. This will be achieved by investigating the rate at which novel traits evolve and patterns of character repetition across a large sample of evolutionary trees.

iii) To investigate whether the tendency for traits to evolve convergently in geographically separated groups of organisms leads to biogeographical patterns being more congruent with molecular phylogenies than morphological ones. If morphological trees are prone to error as a result of convergent evolution from ecological constraints, one would expect them to tend to be less consistant with biogeography than their molecular counterparts.

iv) To investigate whether intrinsic genetic constraints limit evolution. Genome duplications, resulting in plolyploidy, represent the most compelling scenarios for the removal of these constraints and so might be expected to faciliate the evolution of clades in which they occur. More specificially, a difference in 'evolvability' should be reflected in higher speciation after genome duplication events. This study will, therefore, test whether polyploid clades show significantly higher taxonomic diversity than non-polyploid clades.

2 Why Should We Investigate The Morphological Disparity Of Plant Clades?

Jack W. Oyston, Martin Hughes, Sylvain Gerber & Matthew A. Wills

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This paper reports on original research I carried out during my Higher Research Degree candidature. Convergent evolution as a set of processes acts to limit the range of forms that can evolve. In order to understand more fully the wider significance and impact of convergent evolution, we must first understand patterns of morphological disparity, how it relates to diversity and the extent to which organism forms are limited. Surprisingly, there have been relatively few studies that have studied the variation of morphological forms (disparity) across a large sample of groups and those that have dealt almost exclusively with animal clades (Hughes et al. 2013). This paper presents analyses of macroevolutionary patterns of disparity in major groups of vascular plants, as well as reviewing the opportunities plants present as a study group for analyses of disparity and morphological evolution. Like animals, plant clades show a common trend towards early high disparity, strongly suggesting that one of the macroevolutionary manifestations of convergence is a tendency for groups to show a restricted range of forms later on in their evolutionary history.

Author Contributions
JWO: wrote the manuscript, collated plant morphological and stratigraphic data sets, drafted figures and analysed data.
MH: ran disparity analyses and statistics, summarized the disparity literature and drafted figures.
SG: produced clustering plots.
MAW: conceived and designed the study, wrote the manuscript and drafted one figure.

Chapter 2: Statement of Authorship

This declaration concerns the article entitled:								
WHY SHOULD WE INVESTIGATE THE MORHOLOGICAL DISPARITY OF PLAN Ch								
Publication status (tick one)								
draft manuscript		**Submitted**		**In review**		**Accepted**		**Published** ✓
Publication details (reference)	Oyston, JW, Hughes M, Gerber S, Wills MA, 2915- Why should we investigate the morphological disparity of plant clades? Annals of Botany, 117(5) 859-879							
Candidate's contribution to the paper (detailed, and also given as a percentage).	The candidate contributed to/ considerably contributed to/predominantly executed the… Formulation of ideas: 40% study design by MA Wills, JW Oyston wrote discussion formulated ideas on plant d Design of methodology: 20% selected clades (disparity analysis based on published methodology) Experimental work: 80% analysed morphospace data, collated disparity data Presentation of data in journal format: 60% wrote manuscript drafted figures							
Statement from Candidate	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature.							
Signed	Jack Oyston				**Date**	15/02/18		

Review

TITLE: Why Should we Investigate the Morphological Disparity of Plant Clades?

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Abstract

Background

Disparity refers to the morphological variation in a sample of taxa and is distinct from diversity or taxonomic richness. Diversity and disparity are fundamentally decoupled; many groups attain high levels of disparity early in their evolution, while diversity is still comparatively low. Diversity may subsequently increase even in the face of static or declining disparity by increasingly fine subdivision of morphological 'design' space (morphospace). Many animal clades reached high levels of disparity early in their evolution, but there have been few comparable studies of plant clades, despite their profound ecological and evolutionary importance. We offer a prospective and some preliminary macroevolutionary analyses.

Methods

Classical morphometric methods are most suitable when there is reasonable conservation of form but lose traction where morphological differences become greater (e.g., in comparisons across higher taxa). Discrete character matrices offer one means to compare a greater diversity of forms. We explore morphospaces derived from eight discrete data sets for major plant clades and discuss their macroevolutionary implications.

Key Results

Most of the plant clades in our study show initial, high levels of disparity that differ only marginally from the maximum levels obtained subsequently. These plant clades are characterised by an initial phase of evolution during which most regions of their empirical morphospaces are colonised. Angiosperms show remarkably constant levels of disparity through time; a pattern replicated in three large and semi-independent data sets. Conifers furnish the exception, appearing at relatively low disparity in the latest Carboniferous, before expanding incrementally with the radiation of successive constituent subclades.

Conclusions

Many cladistic datasets can be repurposed for investigating the morphological disparity of plant clades through time and offer insights that are complimentary to more focused morphometric studies. The unique structural and ecological features of plants make them ideally suited to investigating intrinsic and extrinsic constraints on disparity.

Key Words: Disparity, Embryophyta, Morphological diversity, Morphospace, Angiosperms, Conifers, Macroevolution, Clade shapes.

Introduction

The number of species within higher taxa, or within clades of a similar age (Magallón and Sanderson 2001), is hugely variable, even for sister groups diverging (by definition) at the same time. While rates and patterns of extinction are clearly influential, some clades appear much more adept at subdividing niche space and speciating than others; even in comparison with their closest relatives. Some groups foster enormous radiations in diversity despite maintaining conservative bodyplans and displaying only modest morphological variety relative to that in their parent clades. Insects, as the best example, have a highly constrained body organisation (a fixed number of appendages and tagmata) relative to other groups of arthropods (c.f. crustaceans and branchiopods in particular), yet constitute over half of all described arthropod species (Mayhew 2007). Similarly, beetles display remarkably conservative organisation within insects, despite their notoriously high contribution to global species richness (Erwin 1997). There is no necessary relationship, therefore, between the number of species within a group (species richness or diversity) and its morphological diversity. Indeed, there are suggestions that a constrained and entrenched bodyplan might actually be conducive to higher diversity (Rabosky et al. 2012).

In order to study the relationship between species richness and bodyplan conservation, we need to quantify both diversity and morphological variety or disparity for large groups. Methods for studying diversity are well established (Peet 1974; Gotelli and Colwell 2001; Benton 2009; Ezard et al. 2011; Mayhew et al. 2012), but approaches for quantifying disparity are less familiar; particularly in the botanical literature (Chartier et al. 2014). While it is possible and informative to study diversity and disparity across clades within the extant biota (or, indeed, in any time slice), insights into the dynamics of their interaction are most fruitfully gained by investigating the trajectories of clades throughout their evolution. Most studies to date have focussed on animals (Foote 1994; Foote 1997; Moyne and Neige 2007; Hughes et al. 2013), but the long evolutionary history (Wellman 2014) and rich fossil record of land plants (embryophytes) make them ideally suited for comparison. Diversity patterns through time within vascular plants have been studied for many years, typically deriving from species-level compilations of originations and extinctions (Knoll et al. 1979; Niklas et al. 1980; Lidgard and Crane 1990; Kovach and Batten 1993; Cascales-Miñana et al. 2010; Cascales-Miñana and Cleal 2012; Cascales-Miñana and Cleal 2014). Results have differed in some details (Niklas and Tiffney 1994), but are broadly consistent in showing i) a radiation of pteridophytes and gymnosperms in the Late Devonian-Carboniferous ii) a gymnosperm dominated flora in the early-mid Mesozoic of comparatively constant diversity and iii) a mid-late Cretaceous to Tertiary diversity increase, due primarily to the radiation of the angiosperms. The presence of

novel morphological features within this group raised the question of whether phases of embryophyte diversification could be explained by the acquisition of 'key innovations' within angiosperms (Endress 2001), seed plants (Rudall and Bateman 2007) and early land plants (Bateman et al. 1998; Renzaglia et al. 2000). Advances in plant phylogenetics have revealed that the timings of many plant radiations do not match the first appearances of hypothesised innovations (Sanderson and Donoghue 1994; Davies et al. 2004; Vamosi and Vamosi 2010), implying instead that the evolution of suites of characters over an extended period of time may enable diversification (Donoghue 2009). The hunt for specific drivers has shifted to focus on either competitive interactions, for example between plants and herbivores (Agrawal 2007; Futuyma and Agrawal 2009) or environmental factors such as climatic change (McElwain et al. 1999; Beerling et al. 2001; Willis and Niklas 2004; Beerling and Berner 2005; Feild and Arens 2007; Boyce et al. 2009; Willis and McElwain 2013).

In marked constrast to diversity, for which temporal patterns have been investigated for many years, there have been only a handful of studies on the morphological disparity of plants (Boyce and Knoll 2002; Boyce 2005; Wilson and Knoll 2010; Feild et al. 2011; Chartier and Jabbour 2014). Disparity analyses have furnished an important means of assessing macroevolutionary patterns in animals for some years, and we believe that their application to plants would be equally insightful.

Aims

This paper has two primary aims. The first is to provide an overview of the methods used to quantify morphological disparity, with particular emphasis on their application to plant evolution. We contrast concepts of disparity with those of diversity or species richness and explain how exploring both trajectories through time can shed light on the evolutionary dynamics of clades. Morphological disparity is usually quantified with reference to the axes of some form of morphospace; an n-dimensional space in which the distances between species or other operational taxonomic units are proportional to some measure of the morphological distances between them. We therefore distinguish between theoretical and empirical morphospaces and discuss their relative advantages and disadvantages for the study of plants. We also explore a variety of potential data sources and consider their relative merits. Particular emphasis is given to character-based empirical methods, which have proved broadly applicable to animal clades at a wide range of taxonomic levels (Hughes et al. 2013), but have yet to be utilized in plants. The second objective is to demonstrate the application of these methods to a select number of published character matrices for major plant groups. We compare and

contrast the observed patterns of disparity through time with those seen in animals and offer a prospectus for future studies of plant disparity.

What is disparity and why should we study it?

The macroevolution of any major clade through deep time can be characterised in a number of ways. There is perennial interest in how diversity changes (Sepkoski et al. 1981; Sepkoski 1997; Sepkoski and Miller 1998), particularly with regards to how species and higher taxonomic richness responds to major physical or biotic changes such as mass extinctions, the opening up of new habitats or the origination of other major groups. Equally fundamentally, we may wish to know how the constituent taxa of a clade are related and may use phylogeny to better inform the patterns above. Increasingly, however, palaeobiologists are also focussing on the manner in which groups diversified morphologically to give rise to new bodyplans or architectures (Fortey et al. 1996). The range or variance of morphological form across species or other taxa is usually referred to as 'morphological variety', 'morphological disparity' or simply 'disparity' in context. Disparity is therefore a property of a sample of taxa rather than of individual species and is also measured relative to some set of quantifiable variables. Trajectories of disparity through time are often different from patterns of species and higher taxonomic diversity and are also difficult to predict from phylogeny.

Although all morphological variety is generated within the context of a phylogeny, diversity and disparity are fundamentally decoupled (Foote 1991a; Fortey et al. 1996; Fortey et al. 1997; Moyne and Neige 2007). Large samples of morphologically very similar species typically have much lower disparity than small groups of morphologically highly dissimilar species. Specifically, numerous basal groups of animals show levels of disparity greater than or equal to their more diverse, derived counterparts (**Fig. 2.1**) (Foote 1992; Foote 1994; Wills et al. 1994; Foote 1997; Wills 1998b) although exceptions exist (Benson et al. 2012). At a coarse level, higher taxonomic diversity (e.g. numbers of orders or classes) tends to be a better proxy for disparity than numbers of species or genera (Foote 1990). Plots of relative disparity through time are therefore often used alongside plots of diversity in order to understand the dynamics of clade evolution more fully.

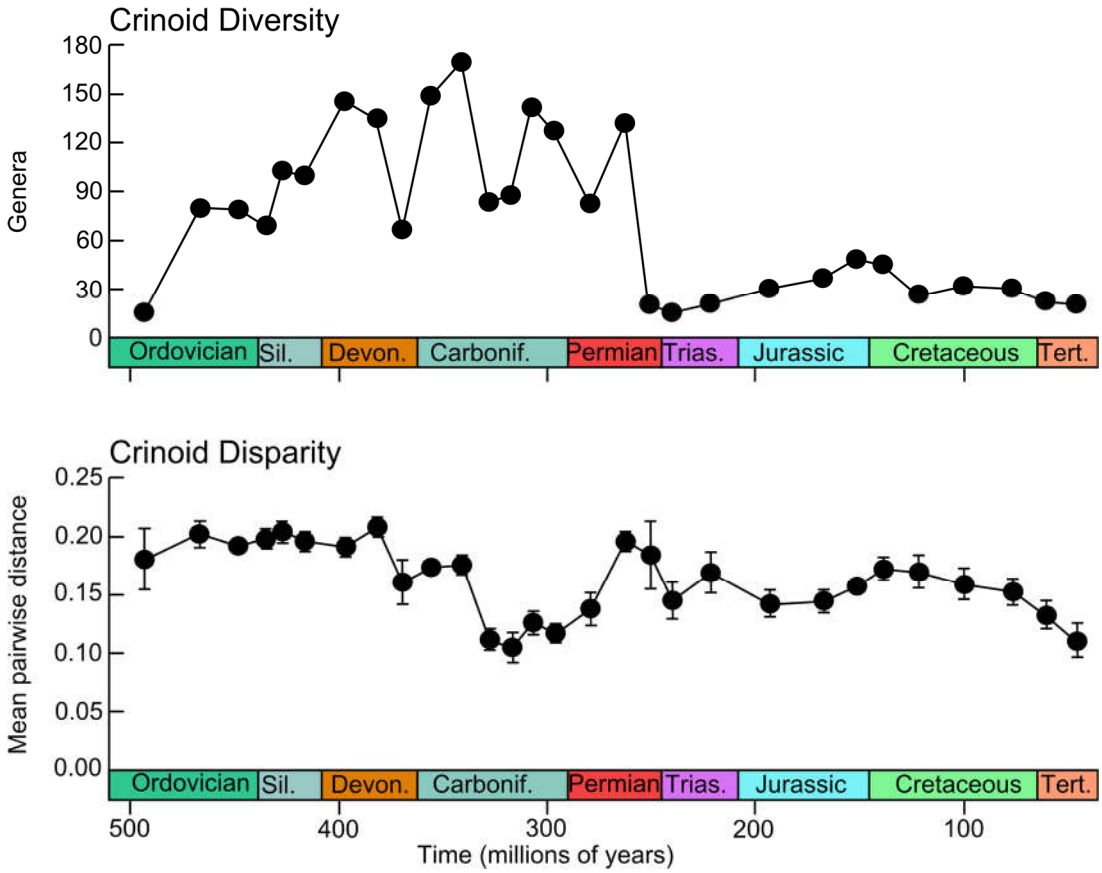

Fig. 2.1 Diversity and disparity are often decoupled, particularly when sampling at lower taxonomic levels. Data for crinoids from Foote (1999). When crinoids first appear in the Ordovician, there are relatively few genera (A), but the mean morphological distances between them (as an index of disparity) are relatively large (B). Part of their subsequent history entailed a systemic increase in diversity through to the early Carboniferous, which paradoxically coincided with a decline in disparity over the same interval. Conversely, disparity remained relatively high for much of the Mesozoic despite a low diversity following the Permo-Triassic mass extinction. Many groups show a similar overall pattern, with relatively small numbers of morphologically distinct species or genera typifying the early phase of a clade's radiation.

Much of the initial impetus for quantifying levels of disparity came from claims about the evolutionary significance of the fossils from the Middle Cambrian Burgess Shale (Whittington 1985; Conway Morris 1989). In particular, it was claimed (Gould 1989) that the range of morphological variety amongst Cambrian arthropods was far greater than that realised at any time subsequently; an argument couched (at least initially) in the perceived higher taxonomic status (i.e., subphylum or class) of many Burgess Shale genera. Gould subsequently propounded an 'inverted iconography' model for the evolution of life (Gould 1991). An initial phase of experimentation and looser constraint on bodyplan evolution was posited to yield early maximal disparity, followed by a phase of winnowing in which most bodyplans were lost and the survivors consolidated and canalised. Subsequent evolution would typically yield few new bodyplans but would see

increases in diversity; increasing numbers of variations (species) upon a more limited number of constrained themes. However, empirical studies of marine invertebrates found that the disparity of Cambrian and recent faunas were essentially equivalent (Briggs et al. 1992; Wills et al. 1994; Fortey et al. 1996; Wills et al. 2012) (**Fig. 2.2**).

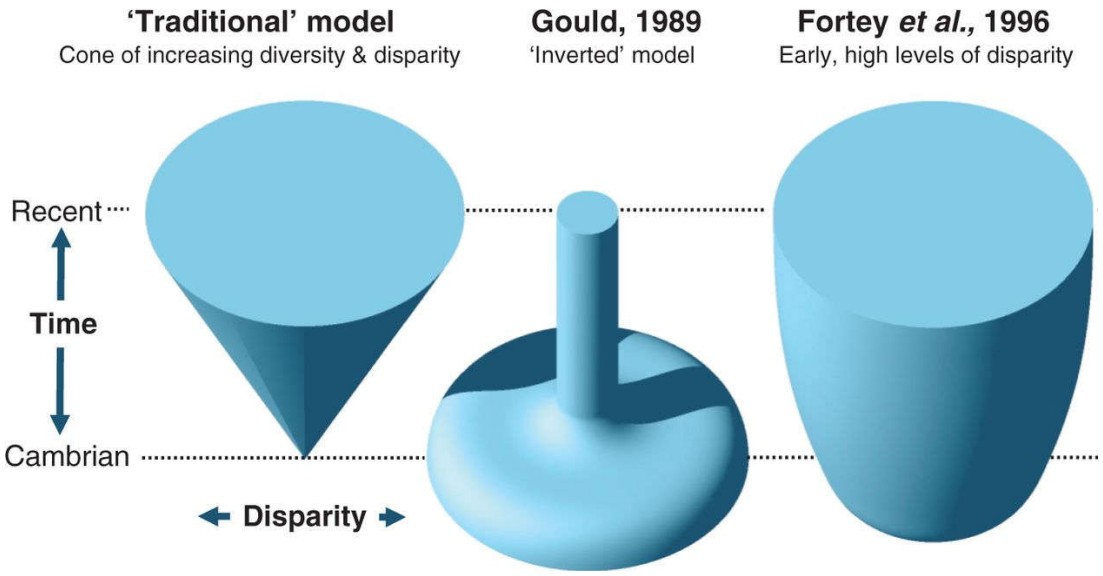

Fig. 2.2 Simplified models of the pattern of morphological disparity through the Phanerozoic. The 'traditional' model assumes that patterns of disparity loosely track diversity, which increases (albeit irregularly) through time. Gould (1989) espoused an inversion of this model, derived largely from his own interpretation of the significance of fossils from the Middle Cambrian Burgess Shale. Cambrian genera were believed to represent numerous, highly distinct bodyplans, between which there were morphological differences comparable to those distinguishing the living phyla. Most of these Cambrian bodyplans were lost arbitrarily in the early Palaeozoic, resulting is a marked reduction in disparity ('decimation'). Subsequent evolution entailed increasing diversity within this more limited number of themes, but disparity was belived to persits unchanged. Fortey et al. (1996) summarised findings from the then-published empirical studies of disparity, which revealed comparable levels of disparity amongst Cambrian invertebrate groups and their living counterparts. Subsequent studies have largely confirmed the validity of the latter picture.

Subsequent studies have examined the disparity of clades at numerous successive time intervals, often demonstrating relatively high early disparity even while diversity is low (Foote 1992; Foote 1994; Wills 1998b). Recently, this approach has been applied to a larger dataset of exclusively fossil animal clades (Hughes et al. 2013). The shape of the disparity profile of a clade through time can be summarised as a centre of gravity index (CG). Clades with precisely symmetrical patterns through time have indices of 0.50, those with higher levels of disparity early in their history have values <0.5 (bottom heavy), while those peaking late tend to > 0.50 (top heavy). In a sample of 98 extinct clades that did not go extinct coincident with one of the 'big five' (Hallam and Wignall 1997; Bambach 2006) mass extinction events, there was a significant bias towards bottom heaviness

and early high disparity. Groups persisting to the present tend to have top-heavy profiles; not least because they are artificially truncated by the recent. Those disappearing coincident with one of the big five mass events tend to be top-heavy, and for similar reasons.

Other research agendas have become increasingly important within particular clades. One is the extent to which bodyplans are modular, and comprise units within which changes are relatively tightly correlated, but between which there is greater flexibility (Klingenberg et al. 2004; Monteiro and Nogueira 2010; Drake and Klingenberg 2010; Cooper et al. 2010) Another is the extent to which developmental versus environmental factors constrain bodyplans over evolutionary time (Allen et al. 2008; Anderson et al. 2011). Increasingly, there is also interest in quantifying functional disparity, notably in fish and basal tetrapods (Friedman 2010; Anderson et al. 2013).

Why study the disparity of plants?

In contrast to animals, there have been few studies investigating the morphological disparity of plant clades. We suspect that the patterns in plants may differ from those in animals; both the trends observed in statistical samples of clades, and the overall pattern of disparity through time for the group as a whole. In this latter context, it may be informative to compare plots of ordinal diversity through time (compiled from Benton, 1993), insofar as counts of higher taxa afford a *very* rough approximation to disparity (**Fig. 2.3**). Animals reach relatively high levels of ordinal diversity relatively early in their history; commensurate with the patterns revealed in explicit studies of disparity. The pattern observed in vascular plants differs markedly. Even accounting for the much later origin of vascular plants compared to animals, plants show a much more gradual increase in ordinal diversity, reaching 50% of their maximum relatively late in their evolutionary history. Plants show ordinal diversity increases in three discrete phases: i) the Late Devonian, corresponding to the initial radiation of pteridophytes and gymnosperms; ii) a smaller increase at the start of the Cretaceous, coincident with the appearance of the angiosperms; iii) a Late Cretaceous increase, corresponding to the appearance of many modern angiosperm groups (Niklas and Tiffney 1994).

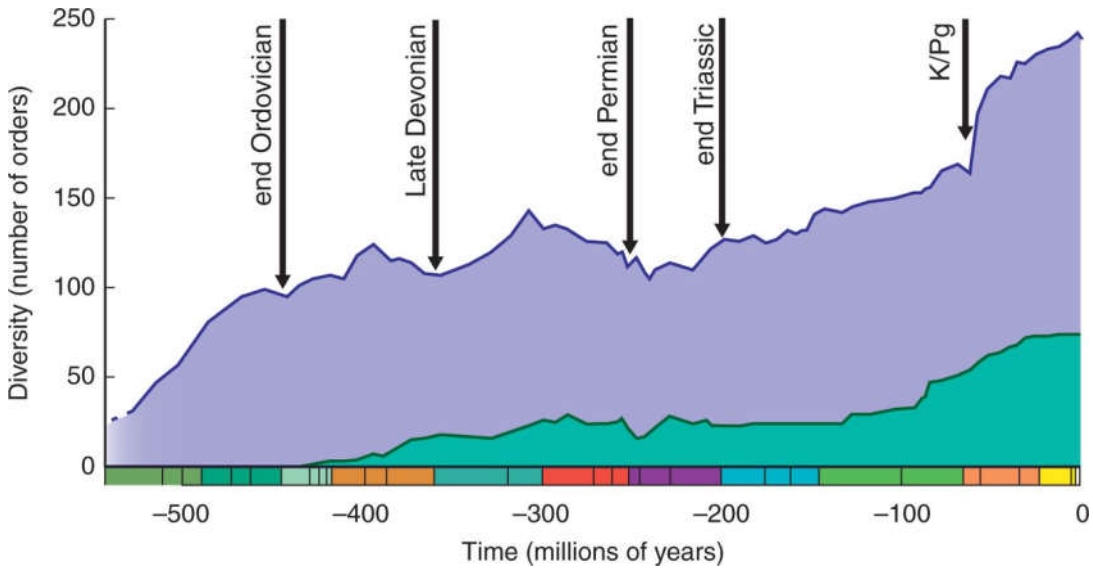

Fig. 2.3 Ordinal diversity of animals (Eumetazoa; blue) and plants (Embryophta: green) through the Phanerozoic. Numbers of orders per geological stage have been tallied from Benton (1993) for animals and from Cascales-Minana and Cleal (2014) for plants. The 'Big Five' mass extinctions are marked with vertical arrows.

Ordinal diversity profiles (**Fig. 2.3**) suggest that vascular plants have fewer fundamentally different modes of morphological organisation than animals and acquired novel bodyplans more gradually. Strikingly, plants appear to be relatively unperturbed by the mass extinction events that were catastrophic for animals; or at least the recovery of plants was rapid enough to mask any significant diversity decreases in the fossil record (Rees 2002; McElwain and Punyasena 2007; Cascales-Miñana and Cleal 2014). Plants therefore appear to have greater resilience to certain types of ecological disturbance than animals (Cascales-Miñana and Cleal 2012); a surprising inference given that many aspects of plant morphology are thought to be tightly mechanically and physiologically constrained to optimise photosynthetic efficiency and structural support (Niklas and Kerchner 1984). Even relatively simple optimization models with a small number of variables can produce the diverse spectrum of habits and gross phenotypes seen across plant groups (Farnsworth and Niklas 1995; Niklas 1999) (**Fig. 2.4**); ecological disturbance may actually serve as a driver for increasing phenotypic diversity. Therefore, although basic structural components (e.g. phytomers in the case of branches) may be relatively morphologically conserved across taxonomic groups, they can nevertheless produce markedly different gross morphologies, even between closely related species or within species.

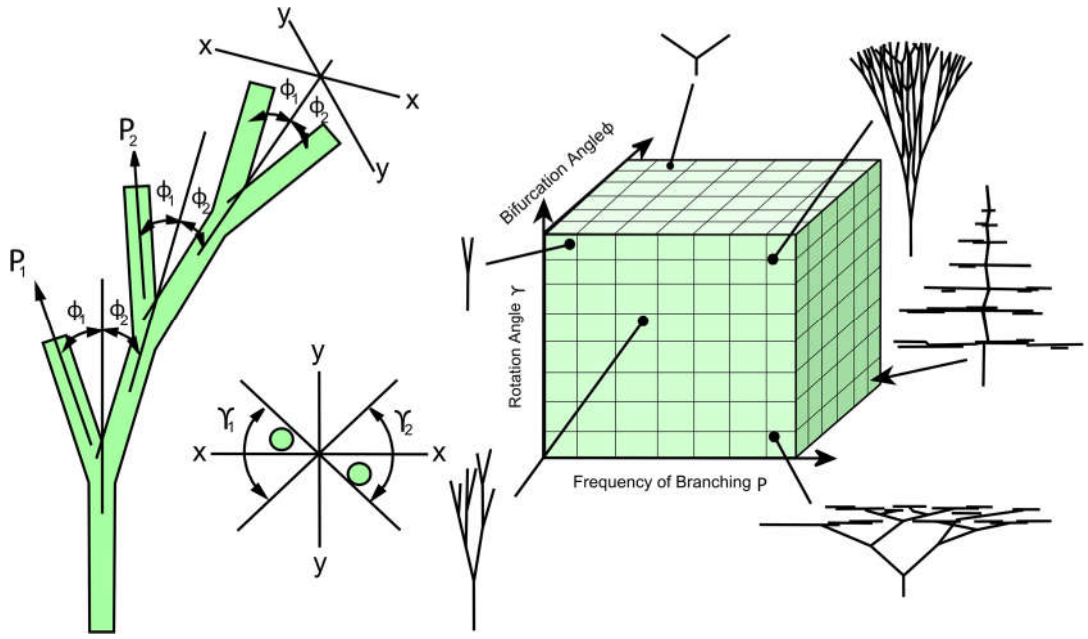

Fig. 2.4 Simulation of bifurcate branching structures capturing aspects of vascular plant morphology (after Niklas, 1999). (A) Illustration of the three parameters used: the bifurcation angle Φ, the rotation angle γ and the probability of apical bifurcation P. Separate numerical values can be used for each parameter for each axes (e.g. P1 and P2). (B) Simplified three-dimensional morphospace created from the orthogonal alignment of the three parameters of the simulation, showing the spectrum of branching structures produced. Cooksonia-type Y-shaped branching structures occupy the upper left region, more complex overtopped structures occupy the lower right rearground, and planated lateral 'branches' occupy the lower right foreground. Figures redrawn from Niklas (1999) with permission from Oxford University Press and the Society for Experimental Biology.

This scale-dependent disparity is one of the defining characteristics of vascular plants and likely facilitates the unparalleled level of phenotypic plasticity seen within many plant species (Schlichting 1986; Schlichting 2002; Bradshaw 2006). The hierarchical modularity in many aspects of plant form (Barthélémy and Caraglio 2007; Klingenberg et al. 2012) may also have profound implications for plant evolution (Friedman and Williams 2003).

Studies of plant disparity to date have mostly focused on specific structures in which shape variation is believed to be of particular functional importance, rather than on holistic analyses of form. Leaf and shoot disparity, in particular, have been extensively studied. Boyce & Knoll (Boyce and Knoll 2002) investigated trends in leaf shape in fossil plant lineages, revealing a rapid expansion of leaf morphospace in the Early/Middle Carboniferous. The genetic controls on leaf shape (Langlade et al. 2005; Chitwood et al. 2014) and compound leaf structures are gradually being better understood (Klingenberg et al. 2012). Leaf shape appears to be correlated with shoot morphology (Lacroix et al. 2003; Jeune et al. 2006), although the importance of selective, functional and historical

constraints in the evolution of these hierarchical systems is poorly understood (Burns et al. 2008). Floral morphology, despite having long been recognised as a critical component of angiosperm disparity (Stebbins 1951) has received relatively little attention until recently (Whibley et al. 2006; Stournaras et al. 2013; Chartier et al. 2014). Similar considerations apply to the architecture of inflorescences (Prusinkiewicz et al. 2007). Other work has investigated the evolution and possible adaptive value of different types of pollen (Lupia 1999; Ressayre and Godelle 2002) as well as physiological properties in the conductive vessels of major seed plant groups (Wilson and Knoll 2010), both floral and general. Rather than attempt to assess disparity from large collations of morphological data, more holistic approaches tend to consider habit and gross architecture (Niklas and Kerchner 1984; Niklas 1999; Silva and Batalha 2011).

The decoupling of diversity and disparity within higher plant clades appears every bit as great as that within animal groups (Yu et al. 2014). For example, the true grasses (Poaceae) and the bromeliads (Bromelilaceae) are both families of angiosperms in the order Poales. However, the true grasses are represented by about 10,000 species (The Plant List 2017) of varying size but generally similar morphology, while the bromeliads contain just over 3,000 species but show huge variation in inflorescence morphology (Benzing 2000; Sajo et al. 2004). It is clear that a complete picture of plant disparity cannot be captured by focussing exclusively on the disparity of specific structures (as there is strong scale dependence) or by using diversity as a proxy. Holistic approaches that use a broad suite of characters sampled over large numbers of taxa will probably constitute the best way of quantifying plant disparity at macroevolutionary scales. Here, we take some preliminary steps in this direction for a sample of higher plant clades.

Types of data

There are many approaches to quantifying morphology (Moore and Moser 1995; Chapman and Rasskin-Gutman 2001; Lockwood et al. 2002), and the most suitable usually depends upon the application and the question being addressed. Where the forms being compared are broadly similar (e.g., typically species within genera or families), a variety of morphometric approaches can be used to derive sets of continuous variables describing shape and shape change, usually with some implicit standardisation for size and orientation (Rohlf and Marcus 1993; Adams et al. 2004) (**Fig. 2.5**). Three-dimensional, landmark based approaches operate by identifying biologically (or functionally) homologous points (e.g., intersections between homologous structures) across all of the species or higher taxa (hereafter ‘operational taxonomic units’ or OTUs) being compared (Marcus 2000; Cramon-Taubadel et al. 2007; Mitteroecker and Gunz 2009).

Outline based methods describe shapes in more detail. This can either be using a more limited number of discrete points (homologous landmarks), possibly interspersed with semi-landmarks to further specify the form (Bookstein 1997; Perez et al. 2006) or using continuous functions (e.g. Fourier analysis) describing shape (Rohlf and Archie 1984; Crampton 1995). Where the forms being compared are more divergent (e.g. across higher taxa) it often becomes difficult to identify a sufficient number of homologous or functional landmarks to capture all but the most limited and conservative aspects of form variation (Bocxlaer and Schultheiß 2010). Here, it is possible to use an array of discretely coded characters, each recognising two or more alternative states, as descriptors of morphological variation (Wills et al. 1994; Wills 1998b). Such data are more flexible but entail more assumptions and potential subjectivity concerning the selection and discretisation of characters and states. The morphospaces that they define also have properties that differ from those derived from continuous character data (Gavrilets 1999).

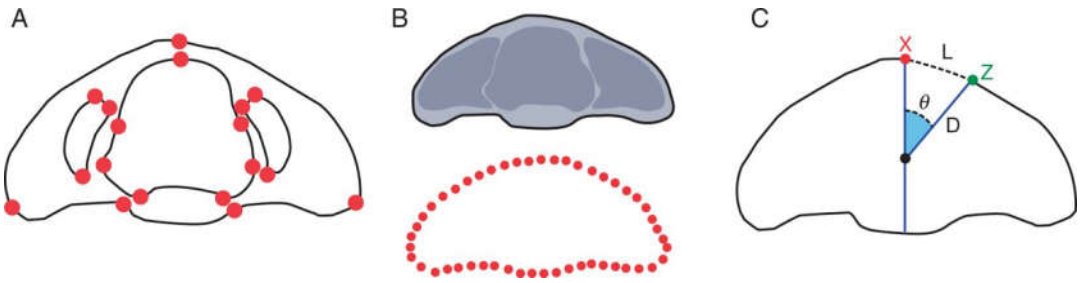

Fig. 2.5 Types of data underpinning disparity analyses. (A) Landmarks (in red) from Webster and Zelditch (2008) situated on homologous points of a trilobite cephalon. (B) Equidistant semi-landmark points (in red) from MacLeod (2011), defining the outline of a trilobite cephalon (shown in grey). (C) Measurements taken for a Fourier analysis of a trilobite cranidium, from Foote (1989). x is the starting point, XY is the midline, point C is the centroid, L is the length from X to Z, D is the distance from the centroid to Z, and θ is the angle XCZ. (B) is redrawn from Semimlandmarks and Radial Fourier Analysis, by Norman MacLeod (2010) Palaeo Maths 101, The Palaeontological Association website (http://www.palass.org/modules.php?name=palaeo_math&page=29) with permission from the Trustees of The Natural History Museum (London).

The first studies that addressed the issue of quantifying disparity explicitly with empirical data sets were published in the late 1980s (Foote 1989; Foote 1990; Briggs et al. 1992; Wills et al. 1994; Foote 1994) (**Fig. 2.6**). The disparity profiles of numerous major animal clades were investigated between then and the end of the decade, before a wane in apparent interest. The last ten years, however, have seen the resurgence of empirical studies, with a particular emphasis on the use of discrete character data sets. As a general rule, metazoan clades tend to show an initial rapid increase in disparity, with early levels of disparity being at or close to the maximum levels observed throughout the group's history.

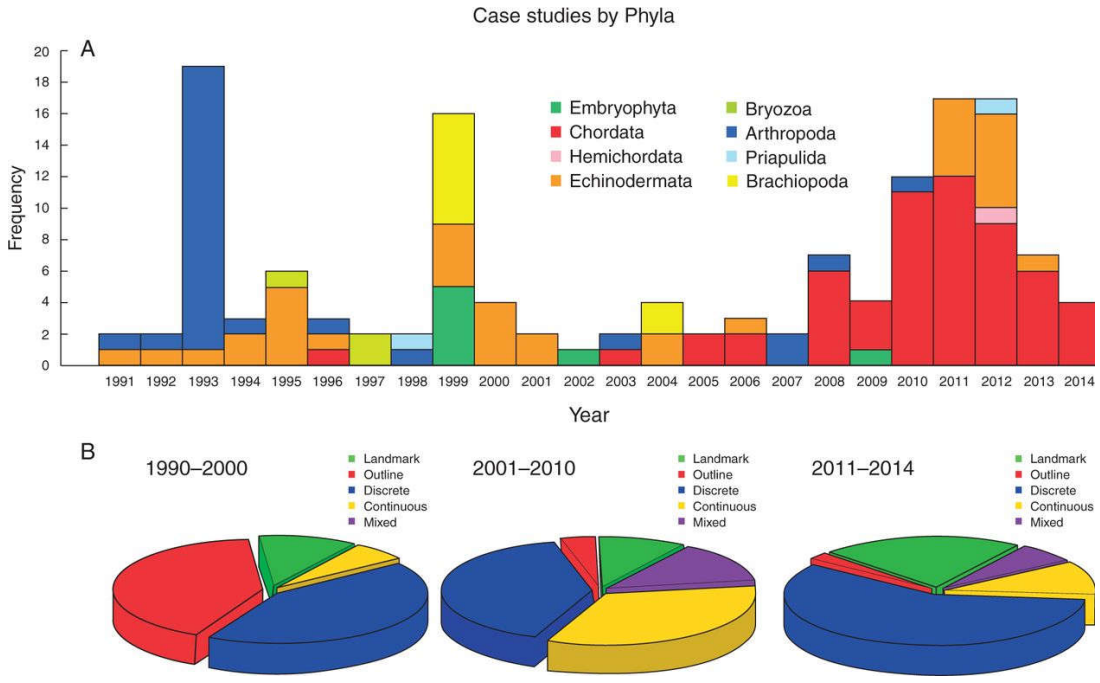

Figure 0.17

Fig. 2.6 The resurgence of disparity analyses for animal clades and the paucity of plant studies. (A) Bar chart of the number and taxonomic distribution of focal clades in disparity analyses from 1990 to 2014. (B) The decline in the use of outline data and the ascendance of discrete character- and landmark-based studies since 2010. We espouse the use of discrete character data for producing empirical morphospaces of disparate plant clades. Underlying data are given in Supplementary Data Table S2. We have removed studies in Hughes et al. (2013) from the figure (this further increases the number of discrete character studies in the last five years).

Biological homology and functional analogy

With all types of data, a distinction can be drawn between those approaches that attempt to capture variation in biologically homologous aspects of morphology (Rohlf 2002; Klingenberg et al. 2004), and those that are more concerned with the functional parameters of shape (Nogueira et al. 2009; Anderson et al. 2011; Figueirido et al. 2011; O'Higgins et al. 2011; Anderson et al. 2013). Morphological disparity can be used to refer to both aspects of variation in form, although the intention is sometimes unspecified (Love 2007). The distinction can be illustrated with reference to the tails of derived sharks and ichthyosaurs, both of which have convergently evolved dorsal and ventral lobes with a relatively high aspect ratio for high-speed aquatic locomotion (Motani 2002; Lingham-Soliar 2005c; Lingham-Soliar and Plodowski 2007). In functional terms, the dorsal lobes of both groups are comparable, as are the ventral lobes. However, the vertebral column of sharks extends into the dorsal tail lobe, while that of ichthyosaurs deviates into the ventral lobe. The tip of both dorsal lobes might therefore constitute a valid functional landmark, but the tip of the dorsal lobe of sharks is *biologically* homologous to the tip of the ventral lobe in ichthyosaurs. Similar considerations apply to discrete, character data; much depends upon the manner in which characters and states are defined.

The exclusive use of putatively biologically homologous discrete variables restricts consideration to the same pool of characters used by cladists. In practice, and especially when dealing with fossil taxa, cladistic homology is established on operational grounds of detailed similarity and relationships to other structures (de Pinna 1991; Butler and Saidel 2000). Such characters may also be functionally analogous, but are not necessarily so (Ruvinsky and Gibson-Brown 2000; Shubin et al. 2009). Cladistic matrices therefore offer a rich resource for quantifying morphological variety across more conservative suites of putatively biologically homologous characters. Moreover, in the absence of homoplasy, we would expect the inter-OTU morphological distances assessed from such data to correlate closely with the evolutionary or patristic distances inferred on most parsimonious or otherwise optimal phylogenetic trees. With the progressive introduction of more character conflict and homoplasy (Sanderson and Donoghue 1989), this correlation will increasingly break down (Kelly et al. 2014), as will the inferred validity of many of the homology statements underpinning the data. Cladograms must account for the distribution of states across taxa by introducing hypotheses of convergence and reversal along branches. The metrics of morphological differences underpinning analyses of morphological disparity do not invoke such hypotheses and are therefore intrinsically more phenetic in approach. Indeed, as levels of homoplasy increase (and more putative homologies are revealed to be analogies),

patterns of morphological variety inferred from homologies and those inferred from statements of functional similarity become progressively more similar.

Morphospaces: theoretical and empirical

Once a set of morphological descriptors or variables has been established for a given group, it is possible to assess the morphological variety of constituent subgroups (e.g. clades) or of chronological subsamples (e.g. taxa from successive geological periods). This can be done directly from the data, but it is more typical to visualise patterns of taxonomic distributions in some form of morphospace; an abstract, multidimensional space in which distances correlate with morphological differences. A distinction (although one not universally embraced; (Mitteroecker and Huttegger 2009)) can be drawn between theoretical and empirical morphospaces. Theoretical morphospaces typically have dimensions that each capture a single quantifiable aspect of form, and (despite being parameterised with reference to real organisms) are defined *a priori* without the need for an empirical data set. The most frequently cited examples are those describing mollusc shells, which variously quantify form and growth using a very modest number of variables (Raup and Michelson 1965; Skalak et al. 1997; Hammer and Bucher 2005; Urdy et al. 2010). Real specimens can be located within theoretical morphospaces, but empirical data are not necessary in order to define them. Empirical morphospaces, by contrast, are constructed from a particular set of empirical morphological data. Their dimensionality tends to be high (Raup and Michelson 1965; Foote 1997; McGhee 1999; Mitteroecker and Huttegger 2009); much higher than that of their theoretical counterparts. For this reason, a number of data reduction techniques (usually multivariate ordination such as principal components or coordinates analysis) are used to condense the dimensionality of the space. This makes it possible to summarise morphological variation using a smaller number of abstracted variables, whilst minimizing distortion. These abstracted axes often cannot be described verbally but may allow the relative disparity of groups to be visualised and quantified more readily. Many of these approaches necessitate a distillation of the multivariate differences between taxa into a single measure of difference or distance for all possible taxon pairs (often realised as a triangular distance matrix analogous to that used to tabulate distances in a road atlas). The precise distance metric used depends upon the nature of the data and the desired properties of the resultant space and/or disparity indices. These complexities are discussed elsewhere at length (Wills 1998b; Wills 2001; Hughes et al. 2013).

Two issues deserve emphasis. Firstly, all morphospaces are abstractions, and necessarily based upon a subset of morphological variables. Variable choice inevitably determines the nature of the space. Many practitioners seek to sample variables as

widely as possible from all aspects of morphology, thereby deriving spaces that reflect overall form. This is not always possible, however, as in many cases where only variation in particular organs or aspects of form can be codified across taxa (Pretorius and Scholtz 2001; Lindbladh 2002; Miller and Venable 2003; Neige 2006; Jones et al. 2009). Morphospaces derived from particular aspects of form or using data from particular organ systems or modules may be well-suited to addressing particular evolutionary questions. However, 'morphological disparity' is usually conceived as referring holistically to overall form. Secondly, indices of disparity are necessarily relative and comparisons are only possible within the parameters of a given morphospace or underlying data set. Hence, while it is possible to make inferences regarding the relative disparity of a group at different times in its evolutionary history, or to compare the disparity of constituent subgroups within an analysis, it is not possible to make comparisons between groups from independently-constructed morphospaces or data sets. This is also the reason why supermatrices uncritically assembled from multiple published data sets (and containing large blocks of inapplicable codes for large groups of taxa) may lose traction on some of the largest and deepest comparative questions.

A variety of disparity indices have been discussed in the literature (Foote 1991a; Foote 1994; Wills et al. 1994; Foote 1997; Wills 2001; Hughes et al. 2013), but it is not our intention to rehearse the relative merits of these here. Among the most widely used approaches are those that distil the dispersion of taxa on multiple axes of the morphospace into a single value. The dispersion on a single axis can be quantified either as the range (defined by the outliers) or the variance of scores; the latter has the advantage of a relative insensitivity to sample size differences. Measures on multiple axes can be combined either as their product – effectively calculating the (hyper)volume of a (hyper)cube – or as their sum. While hypervolumes are superficially more intuitive, they effectively give disproportionate weighting to smaller differences on later axes. Most ordination methods sequester progressively smaller fractions of total variance in later axes but multiplying the univariate indices of dispersion means that halving the spread on any axis (whether the first or last) will halve the resultant hypervolume. Products also collapse to zero whenever the dispersion of taxa on a given axis is also zero. Summing the univariate indices of dispersion (rather than multiplying them) avoids these problems. The sum of variances has particularly desirable properties, therefore, and has been used throughout the present study.

Materials and Methods

Data collection

In general, we followed the protocols set out in Hughes et al. 2013. Morphological matrices for 6 major tracheophyte groups (Angiospermae, Arecales, Nymphales, Pinophyta, Pinaceae and Polypodiales) were selected from the literature. An effort was made to utilise the most recent datasets with even and comprehensive taxonomic sampling. In order to further standardise this sampling, more intensively sampled subgroups were amalgamated, condensing them down to the same taxonomic rank as the rest of the dataset (see Hughes et al. 2013). Some characters were rendered uninformative as a result of these condensations and were therefore removed (specifically; Pinaceae - 46, 47, 51; Arecales - 6, 10, 15, 21, 22, 48, 78, 91, 92, 10; Nymphales - 4, 5, 6, 12, 14, 22, 28, 39, 57). Stratigraphic ranges for constituent taxa were determined from a comprehensive search of the literature, including Fossilworks (Alroy 2013) and The Fossil Record 2 (Benton 1993). Ranges were treated as continuous between first and last occurrences, with data being grouped into stage level time bins. In cases where first and last occurrences were resolved only to intervals above the stage level, we coded for the stage corresponding to the midpoint of the interval. There were very few fossils within the Nymphales, and we therefore estimated ranges using a time calibrated molecular phylogeny (Yoo et al. 2005). Temporal bins with sample sizes of 1 were also amalgamated so that disparity could be calculated for these intervals.

Analyses

For each exemplary clade, intertaxon distance matrices were calculated using the generalised Euclidean distance metric of Wills (Wills 1998b), as implemented in Hughes *et al.* 2013. Distance matrices were ordinated in R (R Core Team 2017) using principal coordinates analysis, and incorporating Cailliez's correction for negative eigenvectors (Cailliez 1983). Disparity for each time bin was calculated as the sum of variances on all axes of the morphospace, yielding a trajectory of disparity through time. The centre of gravity (CG_m) in absolute time (millions of years ago) for each trajectory was calculated as:

$$CG_m = \Sigma\, d_i\, t_i \,/\, \Sigma\, d_i$$

Where d_i is the disparity at the ith stratigraphic interval and t_i the temporal midpoint in absolute time (Myr) of the ith stratigraphic interval. This was then scaled between the ages of the oldest (t_{oldest}) and youngest ($t_{youngest}$) intervals to yield an index of observed CG (CG_{scaled}) between 0 and 1.

$$CG_{scaled} = \frac{t_{oldest} - CG_m}{t_{oldest} - t_{youngest}}$$

Because the time bins were not all of the same duration, the expected CG_{scaled} for a hypothetical clade with constant disparity through time (the inherent *CG* or CG_i) is not necessarily 0.50. We therefore expressed the observed CG_{scaled} relative to CG_i as a baseline; hereafter referred to as simply CG. A bootstrapping test was used to determine whether *CG* was significantly different from the inherent null for a hypothetical clade of uniform disparity (clades for which >97.5% of 1,000 bootstrapped replicates lay either above or below the center of gravity inherent in the timescale (*p*-value <0.05).

An ancillary test was used to determine whether the taxa observed in the first two stages had significantly less disparity than the maximum observed in any time bin. The disparity profile of the clade was bootstrapped 1,000 times. For each replicate curve, the difference in disparity between the first two stages and the disparity maximum was calculated, yielding a distribution. If a difference of zero was within the 95% limits of this distribution, we were unable to reject the null hypothesis: namely that there was no difference between the initial disparity and the maximum (early high disparity). In such cases, maximal disparity was achieved in the earliest stages of the clade's evolution. A similar test was applied to the end of each group's history (late high disparity).

Results and Discussion

Patterns of plant disparity through time

Our results are presented as preliminary explorations of the manner in which our selected clades have explored one form of morphospace through time. While more detailed work will certainly follow, our findings highlight several general patterns and permit certain conclusions.

For extinct clades with homogeneous birth/death dynamics and characters evolving under a Brownian model, the null expectation is that clade disparity profiles should be somewhat top heavy on average (a mean clade CG > 0.5) (Foote 1991a). This is because the morphology of new lineages is contingent upon the morphology of those from which they have evolved; clades would therefore be expected to explore morphospaces in a progressive manner. The extinction of lineages, in contrast, can occur in any pattern with respect to the morphospace. Random extinction, in particular, will tend to maintain a relatively wide morphospacial distribution, introducing a fundamental asymmetry into clade evolution. This is an oversimplistic model for the clades studied here, because all are extant; the Recent effectively truncates their

evolution. As demonstrated by Hughes *et al.* (Hughes et al. 2013), extant clades (as well as those becoming extinct coincident with one of the 'Big Five' mass' events) have a much greater tendency towards top-heaviness merely by virtue of their persistence to the Recent. It is therefore unsurprising that most of our exemplar clades, with the exception of two of the three angiosperm data sets (Doyle et al. 1994; Nandi et al. 1998), show significantly top heavy (CG > 0.5) profiles (**Table 2.1**).

Clade	**Data set**	**Expected *CG***	**Observed *CG***	**Relative *CG***	***CGP*-value**	**Early high**	**Late high**
Angiosperms	Doyle and Endress (2014)	0·757	0·759	0·502	0·001	No	No
Angiosperms	Doyle *et al.* (1994)	0·718	0·722	0·504	0·228	Yes	Yes
Angiosperms	Nandi *et al.* (1998)	0·714	0·718	0·504	0·846	No	No
Conifers (Pinophyta)	Hart (1987)	0·556	0·712	0·655	0·001	No	No
Leptosporangiate Ferns (Polypodiidae)	Pryer *et al.* 1995	0·546	0·669	0·622	0·001	No	No
Palms (Arecaceae)	Baker *et al.* (2009)	0·690	0·761	0·571	0·001	Yes	No
Pines (Pinaceae)	Klymiuk and Stockey (2012)	0·604	0·753	0·649	0·001	No	Yes
Water lilies (Nymphaeales)	Borsch *et al.* (2008)	0·626	0·794	0·668	0·001	Yes	Yes

Table 2.1 Expected (or inherent) and observed centres of gravity (CGscaled) for clade disparity profiles, along with the results of bootstrapping tests (CGP-value) to determine if these differ. The expected CG is that determined for a clade with uniform disparity through time, and deviates from 0·5 because stratigraphic intervals and bins are of variable length. Relative CG is adjusted relative to the expected or inherent CG as a baseline. Clades that persist to the Recent typically have top-heavy profiles, since they are effectively truncated. Early high and late high columns indicate the results of bootstrapping tests to determine if the disparity observed in the first and last intervals is distinguishable from the overall maximum for the clade ('no' indicates a difference with $P < 0{\cdot}05$)

Conifers (Hart 1987) have the most dynamic disparity trajectory, with initial Carboniferous and Permian levels significantly lower than at any subsequent times (**Fig. 2.7**). These modest levels persisted until after the end of the Permian, whereupon there were significant increases into the early Mesozoic. Although disparity appears to decline between the Middle and Late Triassic, it increases subsequently to reach maximum levels at the end of the Jurassic. Levels then decline gradually until the Recent, with extant disparity being significantly lower than the maximum levels observed at the end of the Jurassic. Conifers also show more intensive clustering of taxa in the morphospace at a variety of spatial scales than do the other clades in our study (**Fig. 2.8**). Disparity within the pine family (Klymiuk and Stockey 2012) (**Fig. 2.9**) shows broad similarities with conifers as a whole from their origins in the Jurassic; a reassuring finding given that pines represent a significant proportion of conifer diversity from this time. The initial increase in disparity for pines occurs slightly later than the corresponding increase in conifers as a whole and is maintained until the present day.

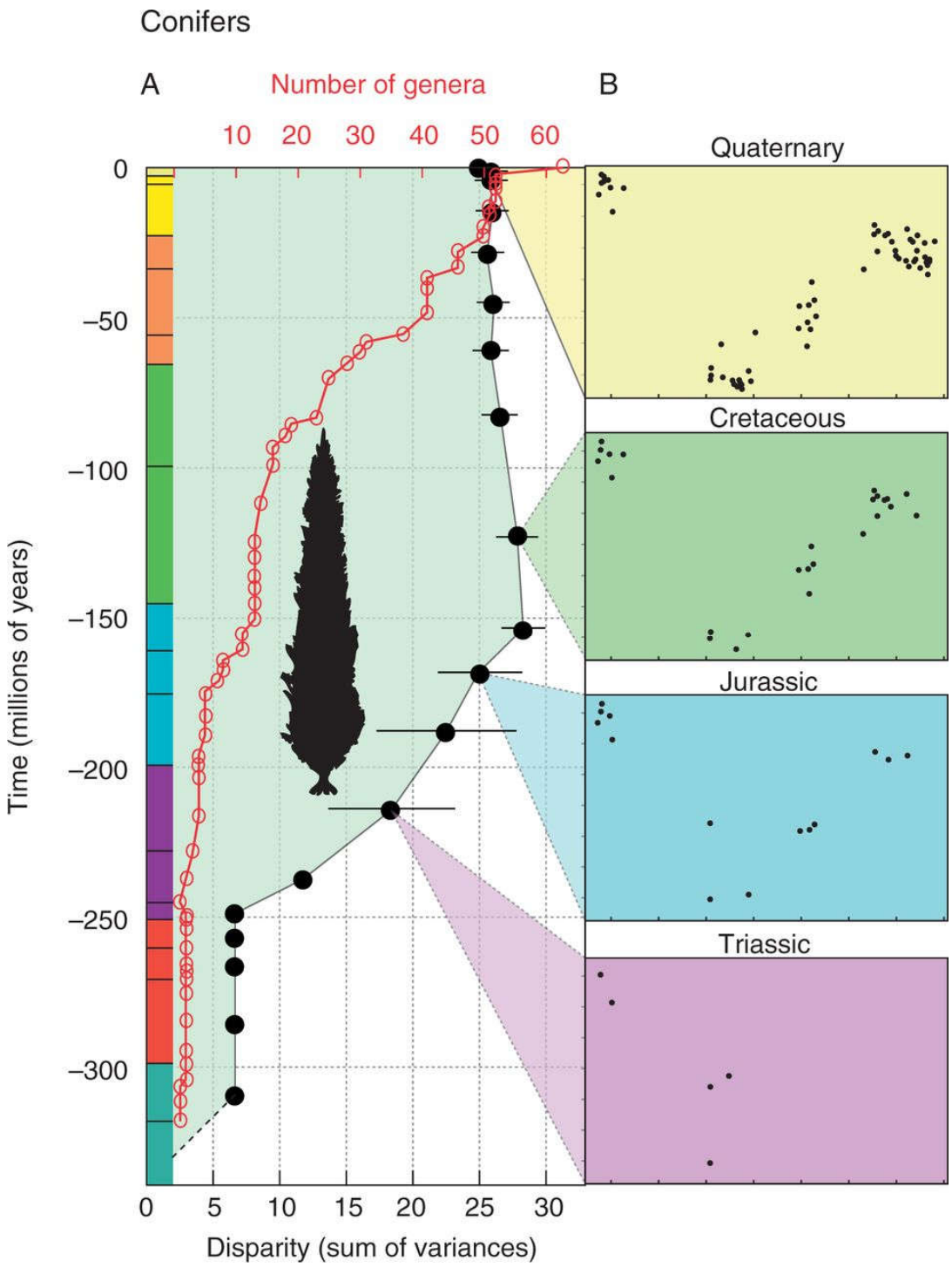

Fig. 2.7 (A) Disparity and diversity profiles for conifers using data from Hart (1987). Disparity (black circles) calculated as the sum of variances on all principal co-ordinate axes within several time bins. Values are the mean of 1000 bootstrap replicates ± s.e. Sampled generic diversity per stage is indicated by open, red circles. (B) Distribution of taxa on the first two principal co-ordinate axes of the empirical morphospace at four of the period time bins.

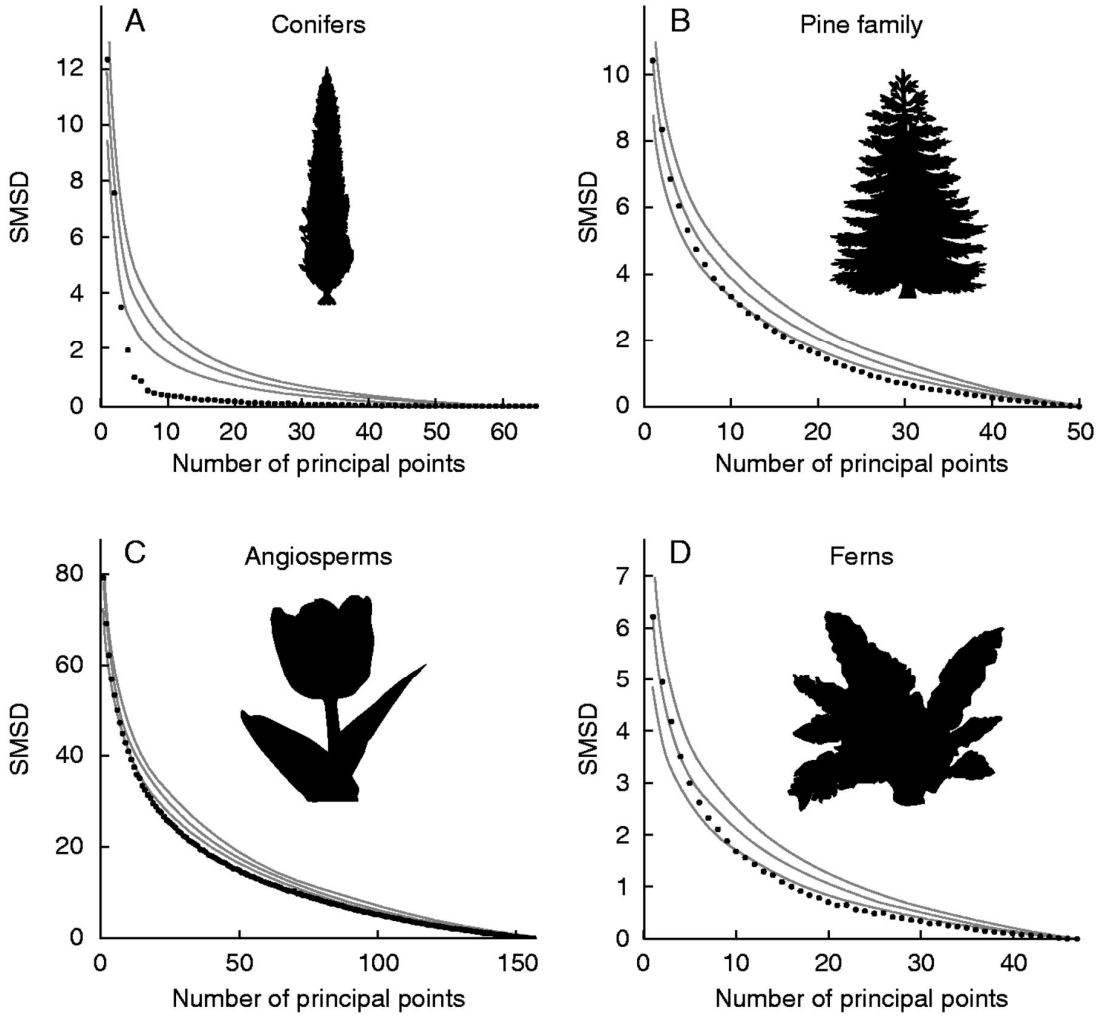

Fig. 2.8 To what extent are taxa clustered within their respective morphospaces at different levels of granularity? Highly clustered, spatially heterogeneous distributions can be approximated with smaller numbers of principal points than can diffuse, spatially homogenous distributions. The extent to which a principal point distribution matches the empirical distribution is given by the sample mean squared deviation (SMSD). Open circles indicate the observed SMSD with an increasing number of principal points. Solid lines denote the expected, null SMSD curve for a multivariate homogeneous distribution containing the same number of points within the same spatial bounds as the observed distribution. Dashed lines are lower and upper bounds of the 95 % confidence interval around this null. Where the observed lines (circles) fall below the dashed interval, the empirical distribution is significantly more tightly clustered than expected. Analyses of four plant morphospaces. (A) Conifers (Hart, 1987), (B) pine family (Klymiuk and Stockey, 2012), (C) angiosperms (Doyle and Endress, 2014), (D) leptosporangiate ferns (Pryer et al., 1995). Note the particularly tight clustering of conifers over a large range of principal point numbers.

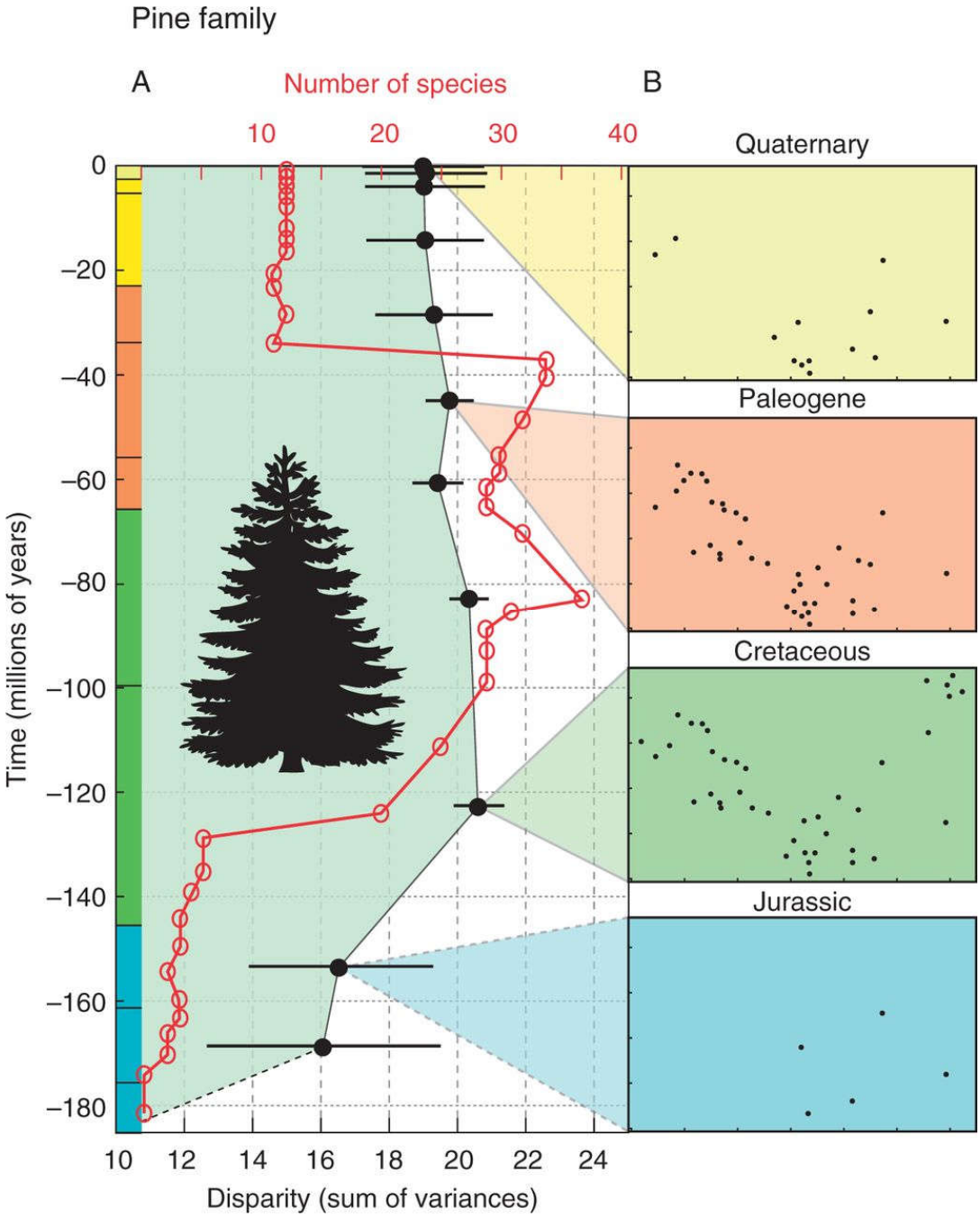

Fig. 2.9 (A) Disparity and diversity profiles for the pine family using data from Klymiuk and Stockey (2012). Disparity (black circles) calculated as the sum of variances on all principal co-ordinate axes within several time bins. Values are the mean of 1000 bootstrap replicates ± s.e. The sampled number of species per stage is indicated by open, red circles. (B) Distribution of taxa on the first two principal co-ordinate axes of the empirical morphospace at four of the period time bins.

Both angiosperms as a whole (Doyle et al. 1994) (**Fig. 2.10**) and the palm sub-clade (Baker et al. 2009) (**Fig. 2.11**) show approximately constant disparity through time. Palm disparity undergoes a slight decrease through the end of the Mesozoic and the early Palaeogene, such that the disparity of living taxa is lower than the realized maximum of the past. In contrast, our results suggest that the water lilies (Borsch et al. 2008) did not reach present levels of disparity until the Neogene (**Fig. 2.12**), with markedly lower levels for the first 10 My of their history. We note that this is our smallest data set (22 taxa), resulting in large estimates of error relative to observed fluctuations in disparity.

In polypod ferns (Pryer et al. 1995), disparity increases through the Permian and Triassic, reaching or slightly exceeding modern levels by the Early Jurassic (**Fig. 2.13**). Disparity increased slightly thereafter to peak levels around the K-Pg but subsequently declined significantly in the last few million years.

An unexpected observation is that high levels of disparity were maintained for the past 80þ My in our largest clades (conifers, pines, ferns and angiosperms), despite successive radiations of sub-groups and catastrophic environmental and faunal upheavals over this time, including the K/Pg event (Ehleringer and Sage 1991; Cerling et al. 1997; Zachos et al. 2001). Indeed, while there is evidence of significant local faunal turnover in plants (McElwain and Punyasena 2007), recent work suggests that only two major extinction pulses are supported in the plant fossil record: one at the Carboniferous–Permian transition and another during the middle-late Permian (Cascales-Miñana and Cleal 2014). Of the groups analysed, only conifers spanned this second event and actually show a significant increase in disparity during this time. It is therefore possible that conifers were evolving into areas of ecospace formerly occupied by other plant groups that declined at the end of the Permian (Retallack 1995).

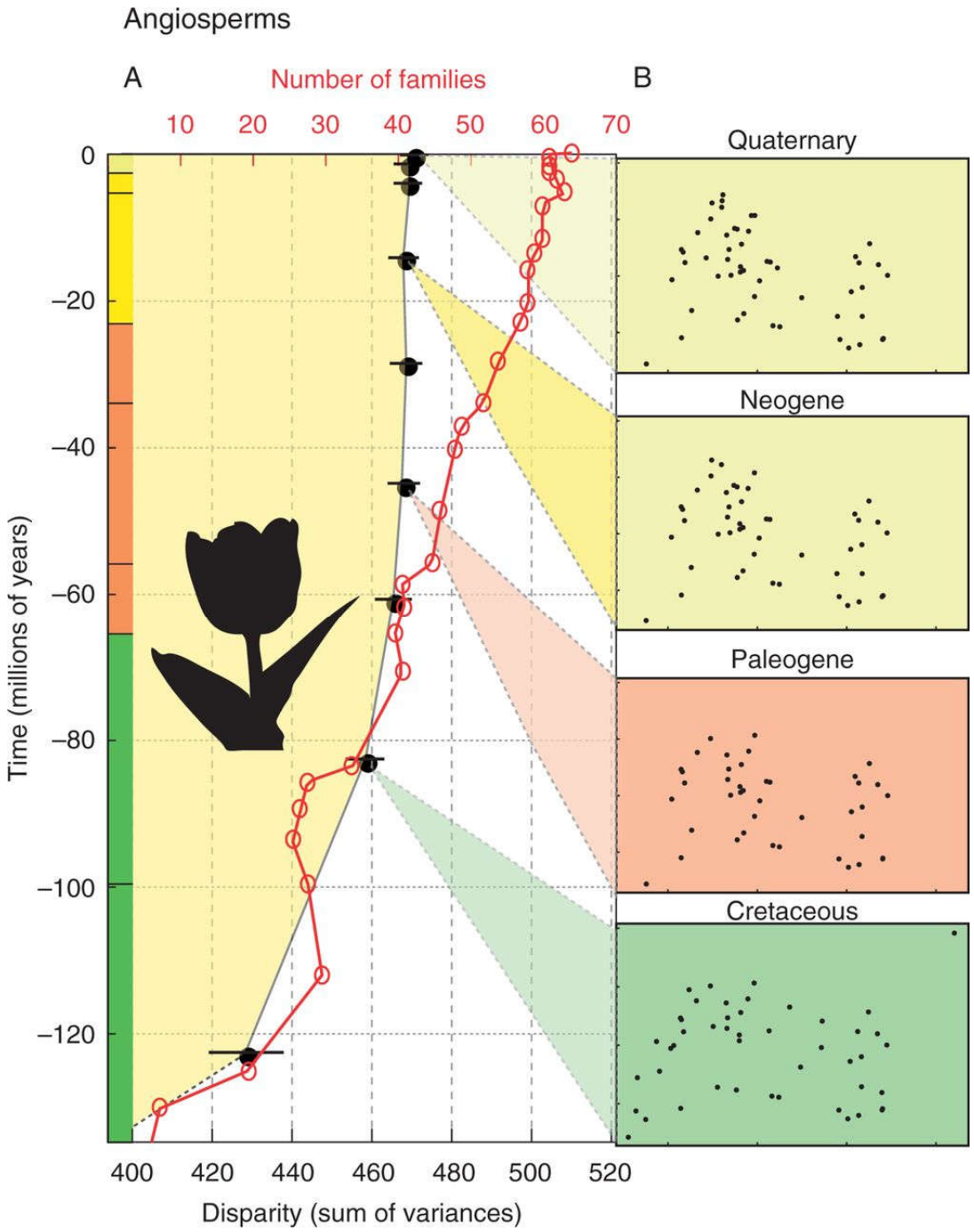

Fig. 2.10 (A) Disparity and diversity profiles for angiosperms using data from Doyle and Endress (2014). Disparity (black circles) calculated as the sum of variances on all principal co-ordinate axes within several time bins. Values are the mean of 1000 bootstrap replicates ± s.e. Sampled familial diversity per stage is indicated by open, red circles. (B) Distribution of taxa on the first two principal co-ordinates of the empirical morphospace at four of the period time bins.

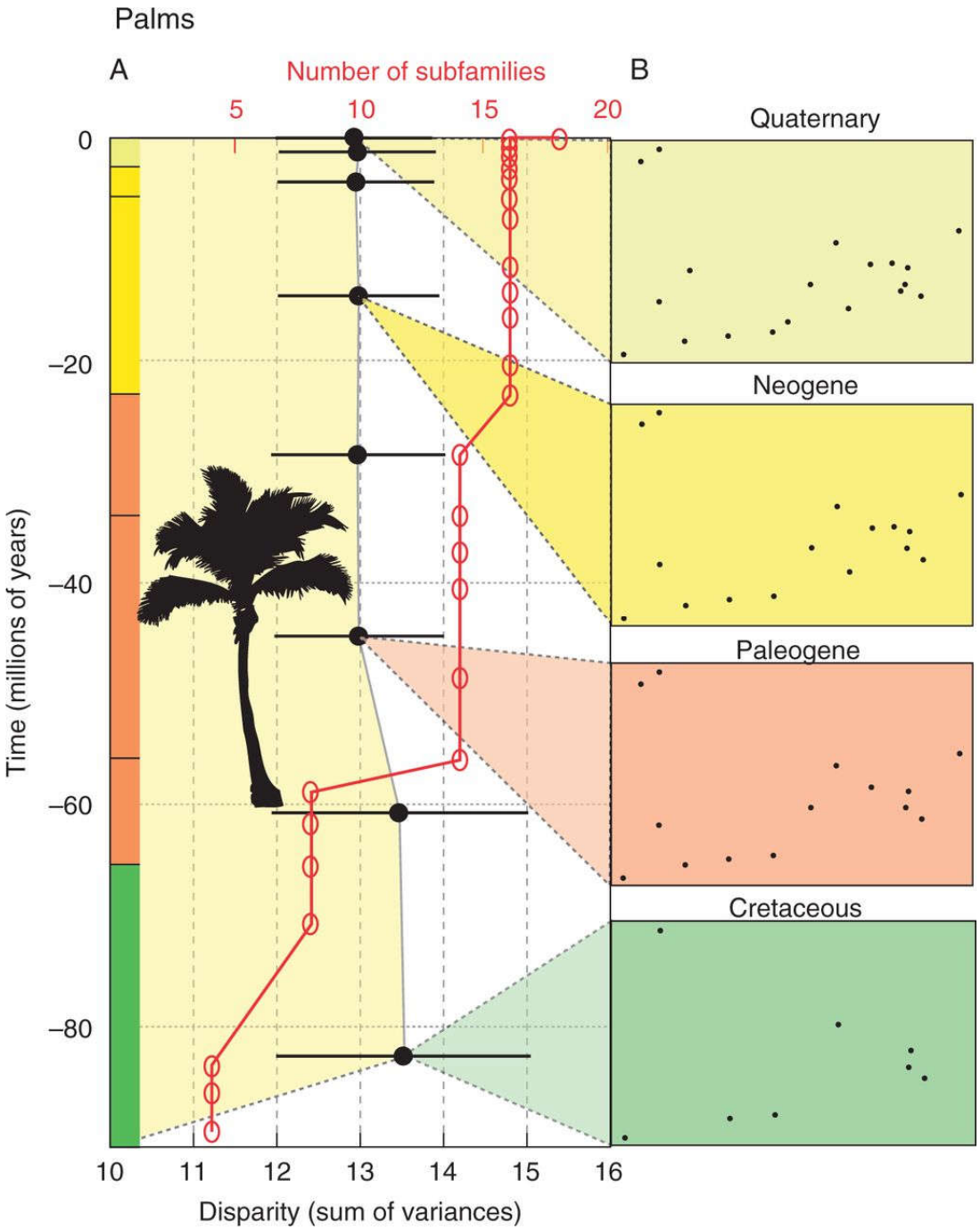

Fig. 2.11 (A) Disparity and diversity profiles for palms using data from Baker et al. (2009). Disparity (black circles) calculated as the sum of variances on all principal co-ordinate axes within several time bins. Values are the mean of 1000 bootstrap replicates ± s.e. Sampled sub-familial diversity per stage is indicated by open, red circles. (B) Distribution of taxa on the first two principal co-ordinate axes of the empirical morphospace at four of the period time bins.

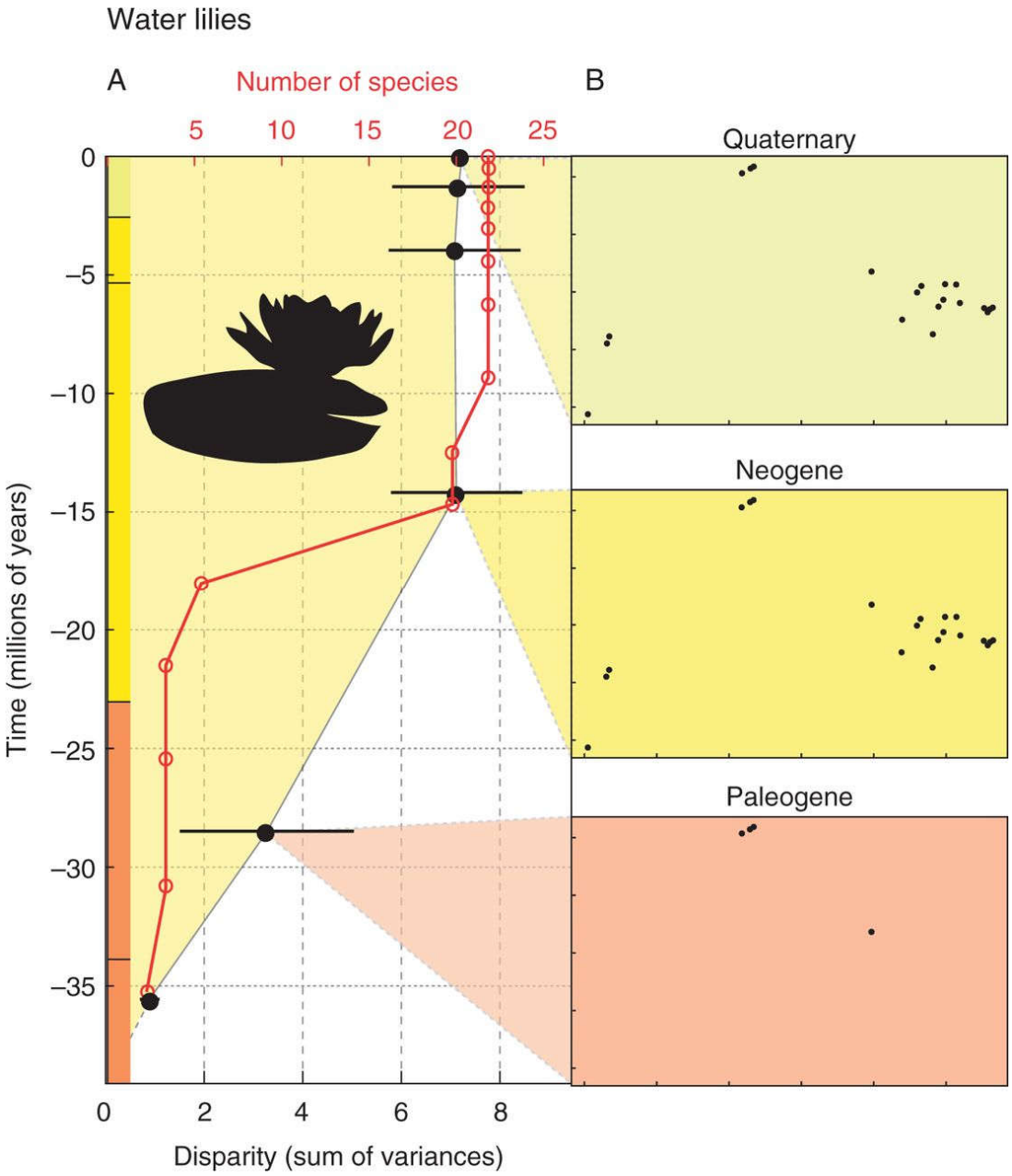

Fig. 2.12 (A) Disparity and diversity profiles for water lilies using data from Borsch et al. (2008). Disparity (black circles) calculated as the sum of variances on all principal co-ordinate axes within several time bins. The sampled number of species per stage is indicated by open, red circles. Values are the mean of 1000 bootstrap replicates ± s.e. (B) Distribution of taxa on the first two principal co-ordinate axes of the empirical morphospace at four of the period time bins.

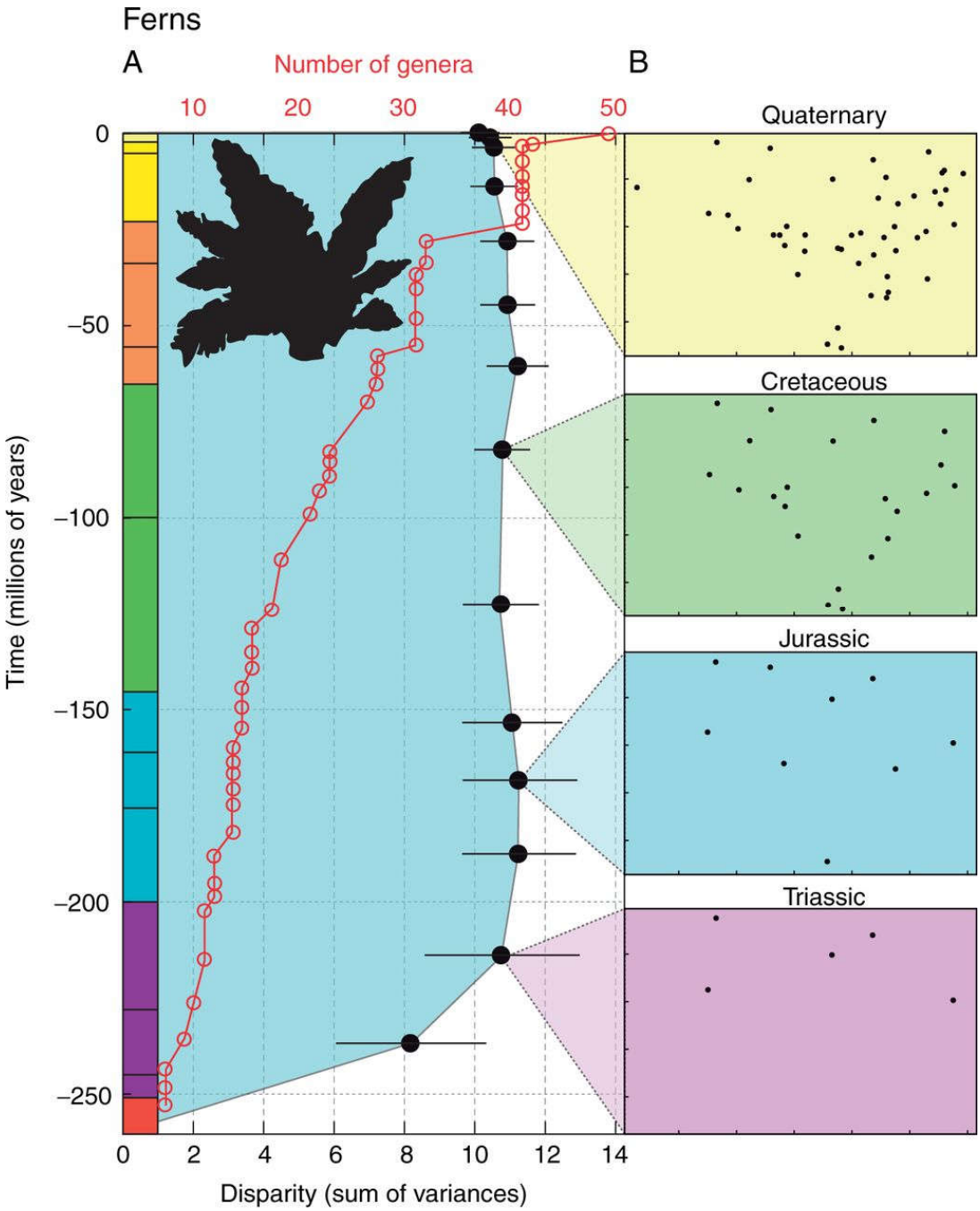

Fig. 2.13 (A) Disparity and diversity profiles for extant leptosporangiate ferns using data from Pryer et al. (1995). Disparity (black circles) calculated as the sum of variances on all principal co-ordinate axes within several time bins. Values are the mean of 1000 bootstrap replicates ± s.e. Generic diversity per stage (from the Paleobiology Database) is indicated by open, red circles. (B) Distribution of taxa on the first two principal co-ordinate axes of the empirical morphospace at four of the period time bins.

The high initial disparity of many of the plant groups investigated here results from the appearance of a small number of morphologically highly distinct taxa close to the base of each clade. In most of our groups, fossils quickly define the extremes of the empirical envelope as soon as they appear, with subsequent lineages gradually filling the intervening morphospace rather than colonizing more eccentric regions of it. Conifers exhibit a rather different pattern (**Fig. 2.7**), with the gradual appearance of sub-clades that each occupy distinct regions of the space (**Fig. 2.8**). Rather than rapid morphospace occupation followed by subsequent saturation, conifers appear to show several phases of morphospace colonization and subsequent diversity increase in tightly defined regions centred around pioneers with novel character combinations. This suggests that the evolution of conifers may have been characterized by the intermittent acquisition of novel morphologies or 'key' innovations, followed by subsequent diversification. Such events may include the radiation of the pines in the Jurassic and the cypresses in the Cretaceous and early Palaeogene. The high degree of morphospace clustering may result from competition with other groups (such as angiosperms), constraining the available morphospace. However, it is more likely to be a function of greater structural or developmental constraints acting upon suites of characters within the conifer data set (moreover, conifers appear to show relatively tight clustering in the Triassic and Jurassic, prior to the inferred appearance of basal angiosperms). Pines show much weaker clustering than conifers as a whole. Characters within the pine data set (Klymiuk and Stockey 2012) were derived from cone morphology, strongly implying that Pinacae were able to explore the majority of possible cone forms rapidly and early in their evolution in a relatively unconstrained manner.

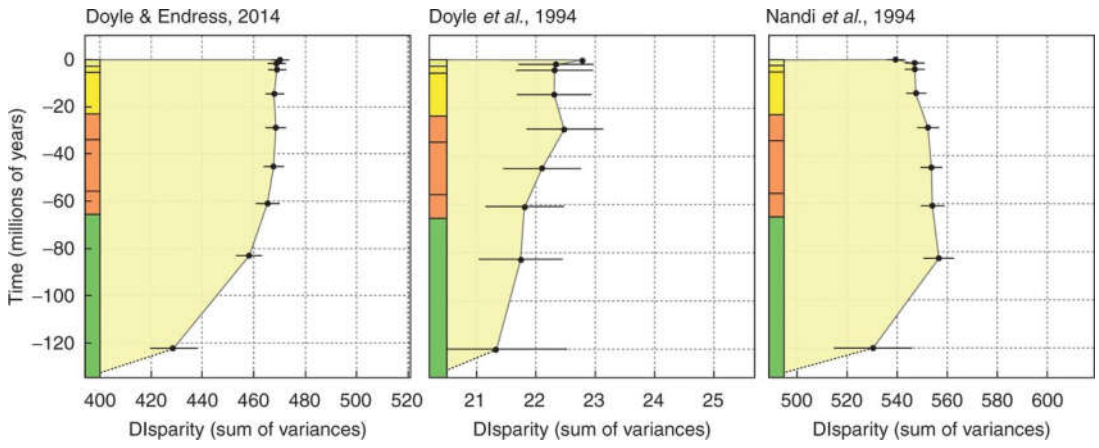

Fig. 2.14 Disparity profiles for three cladistic data sets of angiosperms. Disparity (black circles) calculated as the sum of variances on all principal co-ordinate axes within several time bins. Values are the mean of 1000 bootstrap replicates ± s.e. Despite the inclusion of different taxa and characters, all three profiles show a rapid initial increase in disparity followed by relatively constant disparity over the rest of their history.

Because most of the discrete character matrices analysed here included a broad sample of characters from many different anatomical regions, it is reasonable to assume that the gross morphology of the taxa in the sample was reasonably represented. Our three angiosperm matrices had marked differences in character and taxon composition (**Fig. 2.14**) but showed similar overall patterns of disparity through time.

Why are there so few studies of plant disparity?

There are a number of possible reasons why empirical morphospace approaches have been underutilised within the plant sciences, aside from the usual methodological considerations underpinning the choice of data and indices (Rohlf 1998). Many morphometric approaches entail time-consuming data collection, which may limit tractable sample sizes. There are also difficulties in establishing variable or character sets that can be measured or coded across higher taxa. Most studies therefore focus upon smaller plant clades or else derive data from particular structures (Chartier et al. 2014) rather than investigating overall morphological disparity throughout all plants. Moreover, the often fragmentary nature of fossil material may mean that holistic treatments are impractical, or that many types of morphometric data cannot be obtained (Adams et al. 2004).

Utilising existing discrete morphological data matrices

New morphological character matrices for plants are becoming increasingly rare (Gottlieb 1988; Sytsma et al. 1991); mounting evidence from molecular phylogenetics implies that morphological convergence is obfuscating our understanding of plant relationships (Donoghue and Doyle 2000; Bowe and Coat 2000; Schneider et al. 2009). However, we believe that morphological character data has important uses beyond that of inferring phylogeny (Thorne et al. 2011); not least for quantifying patterns of disparity change throughout morphologically and taxonomically diverse clades with long evolutionary histories. In this context, the problems of homoplasy and convergence that bedevil phylogenetic inference are less marked, since morphospaces are conceived for a variety of purposes and can be intended to reflect a variety of aspects of evolution. We therefore believe that discrete character morphospaces offer a framework for quantifying patterns of morphological disparity within large clades, but also highlight questions that can be addressed in a more focussed manner using other morphometric techniques (Goodman 2002). More comprehensive analyses of existing plant character matrices would represent an efficient use of legacy data, allow some of the commonalities suggested in this paper to be properly tested and would powerfully complement existing and future morphometric studies.

Despite the abundance of discrete, morphological data in the literature, there are a number of considerations when using explicitly cladistic matrices to quantify disparity. Morphological cladists usually seek to resolve phylogeny (Kitching et al. 1998), but are not always concerned with representing accurate branch lengths and evolutionary distances. Even in the extreme approach adopted by pattern cladistics, which views the cladistic method as being divorced from evolutionary assumptions of descent through modification (Brady 1982; Brower 2000), there is still an imperative to recognise hierarchical groupings within sets of taxa (Hennig 1966; Estabrook et al. 1975). There may therefore be a tendency to subdivide morphological variety more finely within taxa that are morphologically conservative in order to resolve their relationships or structure. Conversely, taxa supported by long evolutionary branches may be morphologically very distinct from their nearest sampled relatives, but there may be no imperative to quantify all of these differences to the same degree of resolution as in highly diverse and morphologically similar groups. More generally, it is reasonable to expect character matrices to be biased towards distinctive features and/or those which have been demonstrated to be good at distinguishing groups in previous studies. An allied issue is the assumption that all characters should be treated equally. This may not always be desirable, particularly in cases where some groups are characterised by a limited number of highly distinctive and variable characters while others are defined by broader suites of gross morphological features that are nevertheless coded as a single character. For example, it is probably simplistic to treat the presence or absence of sclereids in the leaves on an equal footing with scandent versus arborescent growth habits (Foster 1956; Rury and Dickison 1984) . While there are a variety of objective approaches for the differential weighting of characters in phylogenetic studies, these are derived from predictions or empirical estimates of levels of homoplasy or the phylogenetic information content of characters (Farris 1969; Sharkey 1989; Goloboff 1993; Goloboff 2014) . In disparity analyses, what may be required is rather some weighting derived from the ontogenetic priority, developmental (Riedl 1977; Arthur 1984; Wimsatt 1986; Arthur 1988) or structural depth (Stebbins 1969; Pettersson 2009) of characters, although such weights are notoriously difficult to assign.

Some cladistic matrices are constructed in order to address particular questions; most commonly sequences of character acquisition across important evolutionary transitions: for example, tetrapods from fishes (Wagner and Chiu 2001; Long and Gordon 2004; Ruta et al. 2006; Wagner et al. 2006) and birds from dinosaurs (Garner et al. 1999; Xu 2006; Brusatte et al. 2014; Heers et al. 2014). Such data intentionally focus on the taxa and characters bracketing these changes, with deliberately much sparser sampling

outside of this. More generally, outgroup taxa – often included for rooting purposes – are more sparsely sampled than those of the ingroups (Graybeal 1998; Heath et al. 2008). Morphological cladistic characters may therefore sample morphological variation unevenly across taxa and through time. Not all data sets are suitable for investigating temporal and taxonomic patterns of morphological variation therefore, and many require some form of moderation. Hughes *et al*, for example, standardised sampling according to higher taxonomy, and removed outgroups (Hughes et al. 2013).

One final issue is the inclusion or otherwise of autapomorphic character states; those present in just a single taxon (Yeates 1992; Bryant 1995). Such states cannot influence inferred cladistic branching structure, but they do affect branch lengths (without introducing homoplasy) and indices of morphological difference. In two-state characters, an autapomophic state renders the entire character cladistically (but not phenetically) uninformative. This property is flagged by most phylogenetic software, which usually results in their removal from cladistic matrices. Autapomorphic states are more likely to be retained in multistate characters (those with three or more states), since the character remains informative overall. More generally, cladists do not actively seek to include autapomorphic states, such that cladistic matrices usually omit this aspect of morphological variation. Empirically, however, the inclusion/exclusion of autapomorphies makes relatively little difference to assessments of morphological variety. The precise effect of autapomorphic states will depend upon the overall properties of the data set and the mode of analysis, but in general they merely cause the taxa possessing them to appear marginally more divergent from the overall mean morphology than they would otherwise be.

There is an increasing desire for large, complete phylogenies to underpin various forms of evolutionary and ecological analyses (Guyer and Slowinski 1993; Phillimore and Freckleton 2006; Tamura et al. 2012). Large matrices of molecular characters (supermatrices) are frequently assembled *de novo* using open data resources and automated algorithms (Liu et al. 2001; Davies et al. 2004; Bininda-Emonds 2004; Davis and Page 2008). There are no similar repositories or tools for morphological matrices. Assembling large matrices comprising hundreds or thousands of OTUs and characters from first principles would ensure greater consistency but is hugely time-consuming. Hence, morphological supermatrices are often assembled by amalgamating the largest data sets or synthetic treatments available for constituent groups. However, this approach may entail its own set of problems. The first is alluded to above; the differential sampling of taxa and characters. Taxon sampling can be standardised more readily, but uniform character sampling requires more detailed knowledge and entails greater

subjectivity. More problematically, it is often difficult or impossible to code many of the characters in the constituent matrices for the 'outgroup' taxa (those represented in the other matrices), thereby resulting in large blocks of inferred plesiomorphies (typically '0' or absent) and inapplicable codings ('?'). Depending upon the manner in which such inapplicabilities are treated, this phenomenon can result in artificially distinct clusters of taxa, strongly but spuriously demarcated by these discontinuities in knowledge and character sampling (Wilkinson et al. 2005; Cotton et al. 2006). For these reasons, large published cladistic matrices compiled from first-hand observations of specimens (or from careful treatments of the primary literature) have many potential advantages over those assembled by conjoining data from disparate published sources (de Queiroz and Gatesy 2007).

Conclusions

1. The concept of morphological disparity is distinct from those of diversity and species richness (Wills 2001) . Indices of disparity attempt to codify the morphological variety of a sample of taxa, are calculated relative to some set of morphological variables or characters, and often utilise a plot of taxa in a multidimensional morphospace. Morphospaces are abstract spaces in which the geometric distances between taxa are proportional to some measure of the morphological differences between them. The nature of a morphospace is entirely contingent upon the underlying data, the manner in which differences between taxa are summarised as distances, and the methods used to project these distances into an *n* dimensional space. The precise approach will depend upon the purpose for which the morphospace is intended. It follows that there is no objective morphospace (in the sense that there is an objective phylogeny), and that the dispersion of taxa in different spaces cannot be compared directly (comparisons between subgroups within the space are possible, but these are necessarily only relative). Morphospaces derived from large samples of characters or variables encompassing most aspects of form are most likely to offer insights into overall morphological variety. Indices of disparity variously assess the relative dispersion of samples of taxa within a morphospace, or provide some distillation of the morphological differences between them.

2. Diversity and disparity appear to be fundamentally decoupled. A significant majority of the animal clades investigated show relatively high disparity early in their evolution (Hughes et al. 2013) at times when diversity is still comparatively low (i.e., there are modest numbers of taxa but these are morphologically highly distinct from each other). The subsequent evolution of such groups often sees an

increase in diversity with little or no concomitant increase in disparity; there are increasing numbers of taxa within a restricted number of morphological ‘themes’. Disparity may even decline as diversity is rising, since some of the most speciose clades have particularly constrained bodyplans but are able to partition ecospace and morphospace particularly finely. A substantial minority of animal clades show other patterns, including high initial disparity at low diversity (Foote 1990).

3. There have been relatively few studies of morphological disparity in plants, and no studies have attempted to assess patterns of overall disparity in major clades through time. Temporal patterns of diversity in plants and animals show significantly different patterns (Knoll et al. 1979), with plants counterintuitively being less affected at times of global mass extinction (Cascales-Miñana and Cleal 2014). An assessment of patterns of disparity in major plant clades is therefore overdue and may provide insights into plant macroevolution to complement those being obtained for animals.

4. There are numerous morphometric methods that allow shape and shape change to be quantified across taxa. However, as the morphogical variety of the forms being compared increases (usually in tandem with the taxonomic scope of the study), the ability of such approaches to compare increasingly disparate forms becomes more limited. Discrete character data sets have certain advantages in this context. There are rich resources of discrete character matrices already available for numerous plant clades, and although initially intended for inferring phylogeny, these data sets can be repurposed for disparity studies within certain strictures.

5. Our preliminary disparity analyses for 6 exemplary plant clades demonstrate that initial levels of disparity are usually high, if not indistinguishable from (or at) the maximum ultimately achieved by the group. Most regions of the morphospace are colonised early in the history of each plant clade, with subsequent evolution serving merely to increase diversity within these regions. The notable exception are the conifers, in which subclades appear intermittently, and progressively colonise distinct regions of the space. This results in conifer disparity increasing incrementally over the first half of the group’s history. All of our exemplary plant clades have disparity profile shapes with a centre of gravity higher than the intrinsic null (significantly so in all save two angiosperm datasets). This is unsurprising, however, since all are extant groups, with profiles truncated by the Recent (Hughes et al. 2013). Combining detailed empirical morphometric studies

of specific anatomical regions with the more holistic approach illustrated here will likely be reciprocally illuminating and offer insights into plant macroevolution.

Acknowledgements

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Contributions

JWO wrote the manuscript, collated plant morphological and stratigraphic datasets, drafted figures and analysed data. MH ran disparity analyses and statistics, summarized the disparity literature and drafted figures. SG produced clustering plots. MAW conceived and designed the study, wrote the manuscript and drafted one figure.

3 What Limits The Morphological Disparity Of Clades?

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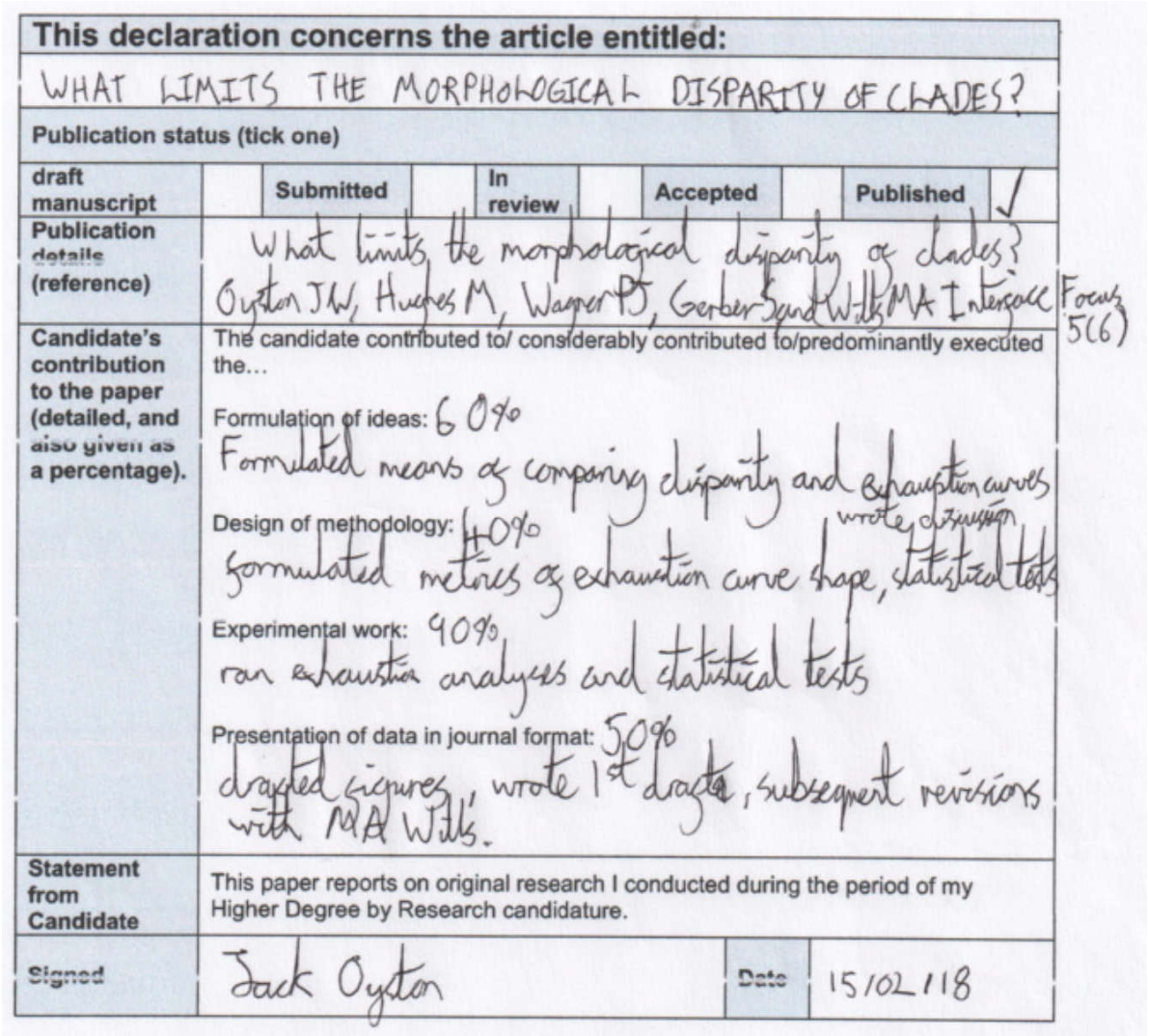
This paper reports on original research I carried out during my Higher Research Degree candidature. One of the most prevalent and important manifestations of convergence at the macroevolutionary scale is that animal and plant groups show a restricted range of forms later on in their evolutionary history (Hughes et al. 2013; Oyston, Hughes, Gerber, et al. 2015). While these restrictions could be imposed by environmental or genetic constraint, it is also possible that these limitations are simply a result of limitations in the sampling of the pool of available morphological characters. The phenomenon of character saturation or character exhaustion has been observed in a range of groups (Wagner 2000) and could drive observed patterns of early high disparity. Although clades with higher overall levels of character reversal and convergence (more homoplasy) reach maximum disparity earlier, this paper found no clear correlation between the amount of character exhaustion and how early or late the clade showed maximum disparity. Patterns of disparity across whole clades, and particularly early high disparity cannot be explained purely as result of sampling from a limited pool of characters. Convergence is therefore likely driven by mechanisms of ecological and genetic constraint which are clade specific, rather than general limitations on the rate at which new characters evolve.

Author Contributions

JWO: wrote the manuscript, collected data, implemented analyses of homoplasy and character exhaustion and drafted figures.
MH: analysed disparity trajectories, collected data, wrote scripts and drafted figures.
PJW: scripted the states/steps analyses and contributed to writing.
SG: analysed disparity trajectories.
MAW: conceived the study, wrote the manuscript and drafted figures.

Chapter 3: Statement of Authorship



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Statement from Candidate	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature.								
Signed	Jack Oyston					**Date**	15/02/18		

What limits the morphological disparity of clades?

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Keywords

Morphological disparity, homoplasy, character states, bodyplan, developmental constraints, ecological restrictions

Summary

The morphological disparity of species within major clades shows a variety of trajectory patterns through evolutionary time. However, there is a significant tendency for groups to reach their maximum disparity relatively early in their histories, even while their species richness or diversity is comparatively low. This pattern of early high disparity suggests that there are internal constraints (e.g., developmental pleiotropy) or external restrictions (e.g., ecological competition) upon the variety of morphologies that can subsequently evolve. It has also been demonstrated that the rate of evolution of new character states decreases in most clades through time (character exhaustion), as does the rate of origination of novel bodyplans and higher taxa. Here we tested whether there was a simple relationship between the level or rate of character state exhaustion and the shape of a clade's disparity profile; specifically its centre of gravity (CG). In a sample of 93 extinct major clades, most showed some degree of exhaustion, but all continued to evolve new states up until their extinction. Projection of states/steps curves suggested that clades realised an average of 60% of their inferred maximum numbers of states. Despite a weak but significant correlation between overall levels of homoplasy and the CG of clade disparity profiles, there were no significant relationships between any of our indices of exhaustion curve shape and the clade disparity CG. Clades showing early high disparity were no more likely to have early character saturation than those with maximum disparity late in their evolution.

1. Introduction

Much like the species and individuals that constitute them, all clades have an origin and all must ultimately suffer extinction. Their intervening histories, however, can follow a variety of complex trajectories. The study of these patterns is central to the study of macroevolution, with questions centring on whether there is a typical pattern (Ward and Signor 1985; Gould 1989; Valentine 1990; Gould 1991; McShea 1994; Wagner 2010; Hughes et al. 2013), whether the fortunes of clades are positively or negatively correlated (Gould and Calloway 1980; Briggs 1998; Sepkoski et al. 2000; McGowan and Dyke 2007; Jablonski 2008; Pedersen et al. 2014) and whether there are particular responses to environmental changes or upheavals (Jablonski 2005). Clade evolution is commonly studied by plotting diversity (numbers of constituent species, genera or higher taxa) through time, which can highlight periods of elevated diversification, extinction and turnover, as well as potential interactions between groups (Benton 1995a; Benton 2001; Smith 2007; McGowan and Smith 2008; Valentine and Jablonski 2010; Ruta et al. 2011). All Phanerozoic diversity curves affirm some form of increasing trajectory, variously modified by physical and biological factors (Benton 2009). Diversity change within individual clades can be modelled using relatively simple birth/death processes with constant parameters (Nee 2006), which predict symmetrical clade shapes – waxing and waning diversity through time – as a null. More complex and asymmetrical patterns result from models in which parameters are varied through time (Foote 1991b; Foote 1993a; Wagner 2010). Gould *et al.*summarised the evolutionary trajectories for extinct clades using a simple measure of their centre of gravity (CG), with a symmetrical clade trajectory having a CG of 0.5 (Gould et al. 1987). Empirical studies revealed a tendency towards bottom-heaviness (CG < 0.5), with clades typically reaching their highest diversity relatively early in their evolution.

1.1 What is disparity?

In addition to assessments of diversity, it is increasingly common to investigate the morphological variety or disparity of clades through time (Erwin 2007; Wagner 2010). All indices of disparity are relative, and depend upon the nature of variables used to quantify form and the manner in which these variables are summarised (Ciampaglio et al. 2001) . Most utilise some form of morphospace; a multidimensional space filling plot in which the distances between taxa are proportional to the measured morphological differences between them (Wills 2001). These may themselves be visualised using data reduction and ordination techniques (principal components or coordinate analyses) to summarise variation in the original set of morphological variables within a smaller number of abstracted axes. Several indices of disparity assess the distribution of taxa in such

morphospaces: for example by adding the ranges or variances on successive axes (a boxing approach), using convex hulls or determining the mean distance between all pairs of taxa. Indices can then be used to compare the disparity of constituent subclades, or to track the morphospace occupation of one or more groups through time, thereby building up a disparity profile (Foote 1992; Foote 1997; Roy and Foote 1997; Wills 1998b; Wills 2001; Wagner 2010) .

Surprisingly, diversity and disparity appear to be fundamentally decoupled (Wagner 2010) . Some periods or clades contain modest numbers of species that are nevertheless highly distinct morphologically, while others contain much greater numbers of morphologically very conservative species. More broadly, some of the most speciose groups (e.g., beetles and insects more generally) have some of the most constrained bodyplans; indeed, there are suggestions that a constrained and entrenched bodyplan might even be conducive to higher diversity (Rabosky et al. 2012). Since clades evolve by lineage branching, we would expect a progressive exploration of morphospace even via a random walk. Once occupied, however, random extinction processes will tend to winnow out the space but are less likely to leave large regions entirely vacant. All other things being equal, therefore, clades might be expected to have top-heavy disparity profiles through time, although driven evolutionary trends and selective extinction patterns may easily combine to yield a diversity of profile shapes. Empirical investigations for major clades over the last twenty-five years also show many different patterns, but the commonest counter-intuitively entails comparatively high disparity relatively early in the clade's history (see also simulations by Foote (Foote 1991a; Foote 1993a; Foote 1996b)). Many groups therefore appear to explore the range of available 'design' options quite quickly, with subsequent evolution principally serving to increase diversity, possibly by the progressively fine subdivision of nîche space (Wills et al. 1994; Erwin 2007; Hughes et al. 2013).

1.2 Why might clades show early high disparity?

One possible explanation for early high disparity is that there are constraints and restrictions upon the available morphospace, thereby limiting the potential for expansion (Foote 1993b; Wagner 1995; Foote 1996a; Gerber 2013) . Once filled, the space can only be subdivided or vacated unless the constraints are removed or a clade evolves so as to circumvent them (Brusatte et al. 2014). Such limits can be broadly classified in four categories: geometric, ontogenetic, physical and environmental.

Geometric constraints are those that can be predicted for any form in any context (many shapes are geometrically impossible) and are not limited to biological structures.

Additional limits are imposed by particular generative processes (Schindel 1990) such that ontogenetic processes can sometimes also be modelled geometrically. In such cases, it may be possible to delimit a morphospace theoretically (McGhee 2006), subsequently plotting real specimens within this. The best-known example is the shell of molluscs (Raup and Michelson 1965). All forms – from simple cones (e.g., belemnites, patelloid limpets and hyolithids) to planispiral coils (e.g., many ammonites and bivalves) and translated coils (e.g., most gastropods) – can be modelled with reference to three or fewer variables that describe growth patterns, defining the theoretical morphospace. Forms outside of this are geometrically and ontogenetically impossible; typically because the shell cannot grow through itself. However, many regions of the theoretical space are never occupied (Schindel 1990). Actualised morphologies are limited to a relatively small fraction of the space, despite the half billion-year history of molluscs, during which time groups have repeatedly re-radiated in the wake of mass extinctions, and within which there is rampant convergence in gross form (Wagner and Erwin 2006; Serb et al. 2011; Smith and Hendricks 2013). Additional limits must apply, therefore. There are more ontogenetic constraints upon form than those predictable geometrically. Organisms develop by the complex interplay of mutually inductive systems and feedback loops, themselves underpinned by cascades of genetic control: not all developmental trajectories and morphologies are possible (Gerber 2014). Further limits to the evolution of disparity are physical, but understanding these requires additional knowledge of biological context. Form is limited by the properties of biological materials, but the performance of such materials depends upon the function of the structures that they compose, and the context and environment in which they are deployed. For example, the physical constrains upon walking (Swartz et al. 1992; Alexander 2003; Zeffer et al. 2003; Palmer and Dyke 2012) and swimming (Koob and Long 2000; Habib 2010) vertebrates differ from an engineering standpoint. Environmental restrictions (Wagner 2010) can therefore be both physical and biological, and might be broadly defined as all those factors that determine the availability of ecospace or niche space. A lineage can only evolve to realise a particular morphology if there are selective advantages; not only to the endpoint, but also to all intermediate forms along that evolutionary trajectory. The physical and biological environments are also dynamic and coupled systems.

1.3 Can we detect the operation of limits on disparity from levels and patterns of homoplasy?

If a clade has evolved to explore the limits of its morphospace, then its constituent lineages variously prevented from exploring novel morphologies might be more constrained or restricted to revisit previously occupied regions. This might be realised as increased levels of character state reversal and convergence. Overall levels of homoplasy might therefore be expected to be higher in constrained clades than in those free to colonise new regions of their morphospace. Most indices of homoplasy are influenced by data set dimensions (Archie 1996), but the homoplasy excess ratio (HER) (Archie 1989) is a relatively unbiased ensemble metric that can be compared across clades (Hoyal Cuthill 2015). Nonetheless, overall levels of homoplasy may be less informative than the trajectory with which homoplastic changes are accrued in transitioning from the root to the terminals of a phylogeny. Wagner (Wagner 2000) noted that the rate of novel character state evolution usually decreased over the lifetime of a clade (Wagner 2000; Wagner et al. 2006; Ruta et al. 2006), with some groups approaching an asymptote and therefore character state exhaustion. If the disparity profile of clades were shaped by such exhaustion patterns, then we might expect clades reaching the bounds of their morphospaces early in their evolution (early high disparity and low CG) to approach an earlier asymptote in numbers of realised states (character state saturation). We therefore test for such relationships here.

2. Methods

2.1 Indices of disparity

Character matrices and first appearance dates (to the stage level) for 93 metazoan clades were obtained from Hughes *et al.* 2013. These discrete character matrices were all sampled uniformly with respect to higher taxonomy, or were edited (by generating composite taxa) in order to standardise coverage (Hughes et al. 2013). See Hughes *et al.* for the discrete character morphospaces, disparity profiles and summary statistics. These authors additionally implemented tests for early high and late high disparity; specifically using a bootstrapping approach to determine if the disparity observed in the first or last two stages could be distinguished from the maximum level attained by the group. The 93 study clades were thereby classified as showing early or late high disparity, and we tested for differences in our indices of homoplasy and character state saturation in these categories using Mann-Whitney U-tests.

A simple index of the extent to which a clade was constrained within its morphospace was derived by expressing the maximum intertaxon Euclidean distance within any time

bin as a fraction of the maximum distance across all time bins. Clades closest to this maximum might also be expected to show higher levels of overall homoplasy and state saturation (Hughes et al. 2013).

Finally, we also derived an index of the degree to which a clade migrated throughout its morphospace during the course of its evolution, since constant levels of disparity through time need not necessarily imply the static occupation of morphospace. We therefore modified the D_{morpho} index of Huang *et al.* 2015, presented below in a slightly more generalized form in equation (1). By standardising the difference in each morphological variable (*MorphV*) of species (*S*) with their median family values (*M*) by the total range of the family values (*R*) the result is an index of the morphological deviation (D_{morpho}), based on Euclidean distance, of species from their family median (Huang et al. 2015).

$$D_{morpho} = \sqrt{\left(\frac{MorphV1_S - MorphV1_M}{MorphV1_R}\right)^2 + \left(\frac{MorphV2_S - MorphV2_M}{MorphV2_R}\right)^2} \qquad (1)$$

The original index used two variables of morphology (size and shape) to construct a two dimensional morphospace. Using equation (1) the authors compared founder species (*F*); defined as fossil taxa believed to be the first instance of their family in the fossil record; with the medians derived from the extant representatives of their respective present day families as seen in equation (2).

$$D_{morpho} = \sqrt{\left(\frac{Size_F - Size_M}{Size_R}\right)^2 + \left(\frac{Shape_F - Shape_M}{Shape_R}\right)^2} \qquad (2)$$

The equation (1) can be adapted as in equation (3) to fit any morphospace consisting of any number of variables (n) as a means of quantifying the degree to which the centroid of the clade moves through the space with time. The value of the statistic gives the deviation away from the centroid of the time slice of interest relative to the position of the one prior to it scaled relative to the size of the space.

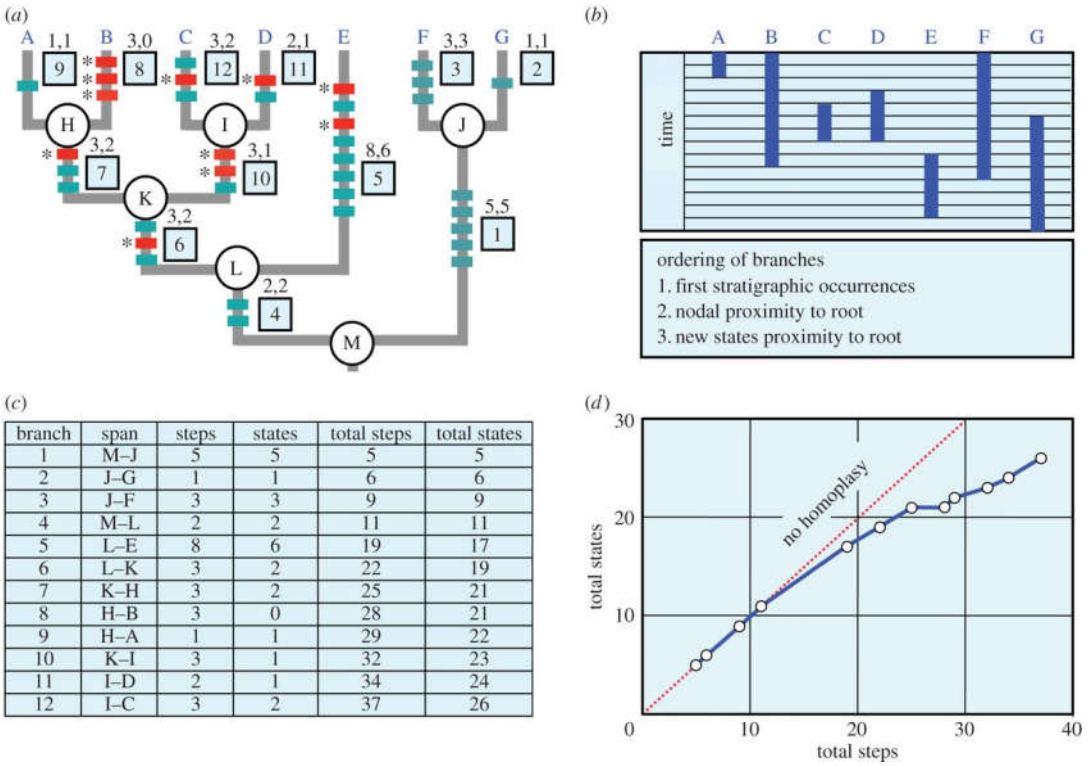
$$D_{centroid} = \sqrt{\left(\frac{PCO_{i,sub,t} - PCO_{i,sub,t-1}}{PCO_{i,Rtot}}\right)^2 + \left(\frac{PCO_{i+1,sub,t} - PCO_{i+1,sub,t-1}}{PCO_{i+1,Rtot}}\right)^2 + \cdots \left(\frac{PCO_{n,sub,t} - PCO_{n,sub,t-1}}{PCO_{n,Rtot}}\right)^2} \qquad (3)$$

For each time bin (*t*), the mean of each principal coordinates (*i* to *n*) are calculated for the subset of taxa (*sub*) found within the time bin. From this value, the equivalent value

for the previous time bin (*t-1*) is deducted from the value for time *t* and result standardised by dividing by the range of all values for principal coordinate *i*. This range equates to the total space occupied across the clades entire history (*Rtot*). The standardized value is then squared. The values for each principal coordinate are calculated and summed and finally square rooted. The final value is the distance travelled through the space by the centroid for the subset of the clade found in each time bin compared to its immediate predecessor. Summing these values produces a value for the degree to which the clade centroid has moved through the space. Due to the nature of the index, the beginning value will always be zero. To account for missing time series data, whenever a gap of time was presented (no fossils found within an interval) the morphospace of the previous interval is used. Therefore, in the absence of extra information, the centroid of the space is deemed to have not moved.

2.2 Phylogenies and indices of homoplasy

A single outgroup taxon was used to infer ancestral character states at the base of each focal ingroup clade. Phylogenies were inferred in TNT using a constraint and random sectorial searches with 10 replications, 5 iterations of drifting and 1 round of fusing. This was followed by tree bisection and reconnection (TBR) searches. The resulting most parsimonious trees (MPTs) sometimes differed from those in the source publications, especially where the taxon sample had been reduced. In cases where multiple MPTs were obtained, we selected the tree most congruent with that presented in the original publication. The character exhaustion analysis required fully resolved (dichotomously branching) trees, so polytomies were resolved stratigraphically. It has been demonstrated that the precise trees used in character exhaustion analyses have relatively minor effects upon the results (Wagner 2000). Moreover, using incorrect MPTs introduces a conservative bias because they minimize the number of steps required to achieve the observed number of character states; longer trees (even if more accurate) necessarily imply greater exhaustion by implying that greater “sampling” of character space fails to yield additional novel states. Overall homoplasy levels were assessed using the homoplasy excess ratio (HER) of Archie (1989); an index that is relatively insensitive to differences in data matrix dimensions. Five hundred randomly permuted matrices were used in each case, each subjected to TNT searches as above.



branch	span	steps	states	total steps	total states
1	M–J	5	5	5	5
2	J–G	1	1	6	6
3	J–F	3	3	9	9
4	M–L	2	2	11	11
5	L–E	8	6	19	17
6	L–K	3	2	22	19
7	K–H	3	2	25	21
8	H–B	3	0	28	21
9	H–A	1	1	29	22
10	K–I	3	1	32	23
11	I–D	2	1	34	24
12	I–C	3	2	37	26

Fig. 3.1 Generating character saturation curves. (a) Step 1: ancestral states are reconstructed on a phylogeny in order to determine character transitions along each branch. Horizontal bars on branches indicate character state changes. Asterisks denote homoplastic changes (steps) that are not also new states. Branches are numbered within squares, and pairs of numbers above these indicate number of steps and number of novel states respectively. (b) Step 2: branches are ordered by stratigraphic occurrence, proximity to the root and number of new states. (c) Step 3: the number of steps and new states along each branch in the resulting sequence (denoted by the values in boxes) are calculated, along with running totals. (d) Step 4: the cumulative total of new states is plotted against the cumulative total of steps to generate a saturation curve. The dotted line indicates the trajectory (gradient of 1.0) for the hypothetical situation where there is no homoplasy, and all steps are novel states.

Character exhaustion analyses were performed using the method of Wagner (Wagner 2000) (**Fig.3.1**). Character states for ancestral nodes were reconstructed using Fitch parsimony (Fitch 1971) and all nodes were numbered. A traversal of the tree from the root to the terminal branches was used to tally a cumulative total of character change steps and novel states. Working from the basal node, branches were added in order of their stratigraphic age (as given by the age of the oldest fossil representative of the clade the branch leads to), then by their nodal proximity to the root, and finally according to the smallest numbers of novel states evolving along them. As fossil data are unavailable for unsampled internal nodes, many of the internal branches could not be ordered by stratigraphic age and so were ranked according to the last two criteria. This does leave ties. For example, consider six taxa that appear in the same stratigraphic interval with

hypothesized relationships ((A,(B,C)),(D,(E,F)). The basal node necessarily precedes the (A,(B,C)) and (D,(E,F)) nodes, and those two nodes necessarily precede the (B,C) and (E,F) nodes, respectively. However, neither the (A,(B,C)) nor (D,(E,F)) sister nodes necessarily precede each other (Wagner and Sidor 2000), and the 'cousin' nodes (B,C) and (E,F) cannot be ordered relative to each other either. Therefore, such sister-taxon and 'Xth cousin' ties were resolved randomly, but with second cousin nodes preceding third cousin nodes. This ordering strategy is the most exact possible without recourse to stratigraphic data of higher resolution to subdivide branches. Such data are unavailable for the vast majority of our sampled clades. In addition, it is not uncommon for multiple fossil taxa to have their first occurrences at the same locality, resulting in ties, regardless of the temporal resolution available. Another approach would be to use arbitrary evolutionary models to calibrate branch lengths (Lewis 2001; Ronquist and Huelsenbeck 2003; Nylander et al. 2004), and to assign character changes between known occurrences (Lloyd et al. 2012). However, such models will bias results towards favouring character exhaustion. Longer branches with more novel character states will be pulled closer to the root, causing novel states to appear earlier in evolutionary time. This will be more pronounced if rate-variation among characters is permitted, because characters with a greater number of novel states will evolve at a faster rate, thereby concentrating the novel state changes on branches with deeper divergence times. In addition, it has been shown that different branch scaling methods can markedly influence the evolutionary inferences derived from trees (Bapst 2014). Our approach is therefore a conservative one, insofar as it is more likely to defer the appearance of novel character states until later in our character exhaustion curves (inferred exhaustion will be less marked) and is not contingent upon arbitrary models of character evolution.

For each branch in the ranked sequence, the total number of character state changes (steps) and the total number of novel character states (states) was calculated and added to the cumulative total. Plotting the cumulative number of steps against the cumulative number of states yielded a states/steps curve for each of the 93 clades.

All subsequent analyses were implemented in R v. 3.0.1 (R Core Team 2017). The shape of each states steps curve was quantified in two ways (**Fig. 3.2**). First, we recorded the fraction of total observed steps at which an arbitrary threshold (50%) of the maximum number of observed states was reached. Second, we calculated the centre of gravity (CG) for each states/steps curve (in an analogous manner to the CG for disparity profiles) and scaled this relative to the number of steps in the clade. The most convex curves with the highest initial gradients (i.e., those more quickly approaching an asymptote) yielded the lowest values for both indices. We also estimated the overall degree of saturation at

clade extinction by fitting Michaelis-Menten like non-linear regression curves (Dowd and Riggs 1965; Soberon and Llorente 1993; Hsu et al. 2001) to the data based on the assumption that the number of character states would eventually reach an asymptote (i.e., that the character space was finite). We then expressed the maximum number of observed states as a fraction of the inferred maximum. Low values in this context indicated clades that were further from saturation at their extinction.

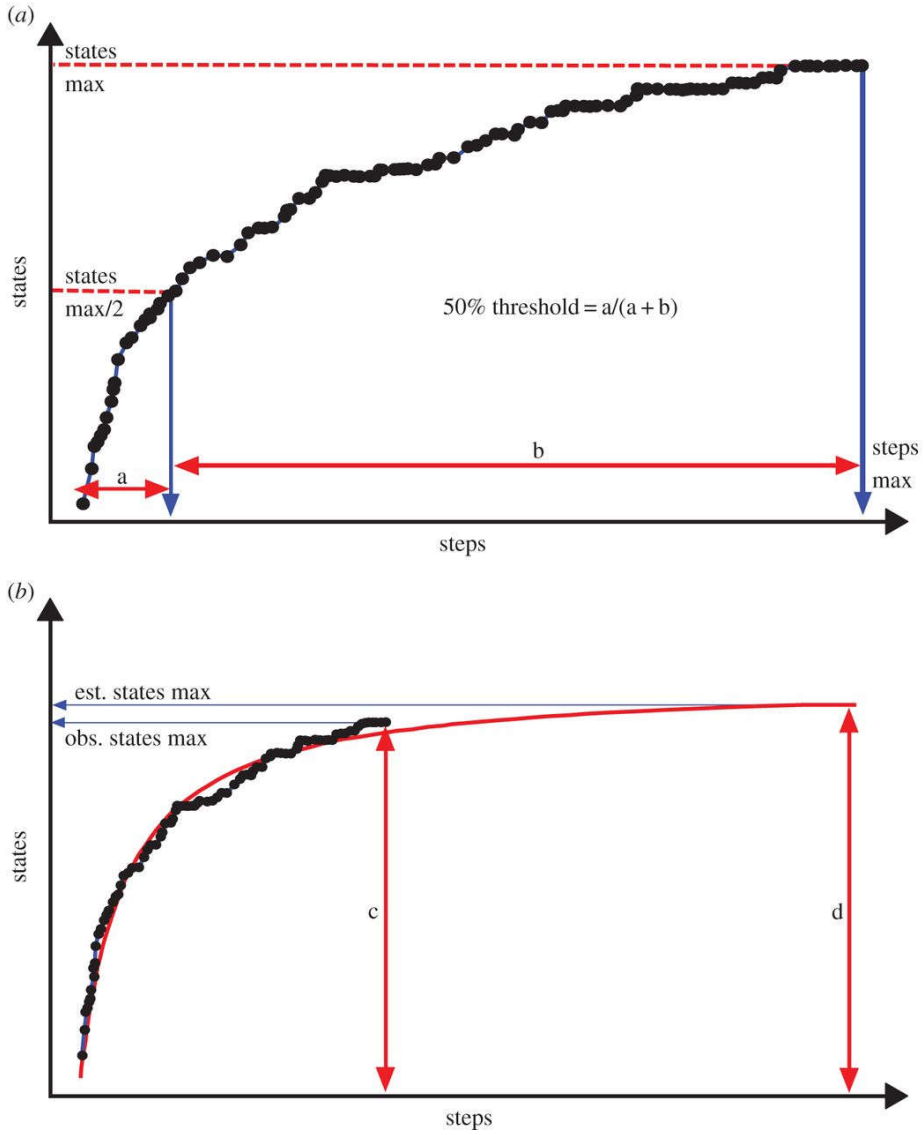


Fig. 3.2 Quantifying character saturation from state/steps curves. (a) The 50% threshold is defined as the number of steps taken to reach 50% of the total number of character states (a) divided by the total number of observed steps (a + b). (b) The fraction of maximum states is defined as the total number of observed character states (c) divided by the estimated maximum number of possible character states (d) from the asymptote of the Michaelis–Menten curve.

Finally, each dataset was fitted to Wagner's idealised models of character evolution (Wagner 2000). Log-likelihood values were used to assess whether a null model of a step-independent (linear) model of character evolution could be rejected in favour of either of the character exhaustion models.

3. Results

All summary statistics are given in **Table 3.1**. Of our 93 sampled clades, only two realised the maximum intertaxon Euclidean distance for the entire morphospace within a single time bin. Most appeared relatively free to evolve within the morphospatial bounds, with a mean maximum observed distance as a fraction of the maximum possible of 0.712. Homoplasy excess ratios (HER) had a mean of 0.470 with a fairly typical distribution (Archie 1989; Archie 1996). States/steps curves exhibited a range of shapes although most were asymptotic and reached a slope less than 1 (**Fig.3.3**), indicating that some degree of character state saturation occurred in most groups. Of the 68 clades tested for fit with Wagner's models, the null model of a linear increase in new character states was rejected in 60 cases. Although nearly all clades showed a decrease in the rate at which new states appeared after a modest number of steps, a small number maintained a much reduced but constant rate of addition of states over the remainder of their evolutionary history (e.g. cinctans, **Fig. 3.3**, panel C). Some groups, such as Aplodontoidea (Mammalia) (**Fig. 3.3**, panel F), had stepped patterns, indicating that the origin of novel states was concentrated in a relatively small number of branches equidistant from the root. This is similar to the pattern recently documented within post-Paleozoic echinoids (Hopkins and Smith 2015). The mean fraction of steps at which 50% of states were realised was 0.307, with values ranging between 0.103 (the most convex curve with fastest saturation) to 0.625 (the most nearly linear curve with the least saturation). Michaelis-Menten curve fits all inferred asymptotes in excess of the realised maximum at extinction; observed maxima varied between 0.067 and 0.896 of the inferred, with a mean of 0.583. These two indices of state saturation were strongly negatively and highly significantly correlated (r_s = -0.873, $p < 0.001$) (those clades taking longest to reach 50% of the realised maximum tended to be those in which the realised maximum was the smallest fraction of the inferred, since the empirical curves were truncated by extinction at the steepest gradients). Centre of gravity (CG) indices for the empirical curves showed a narrow range of values as expected (0.571-0.704), but correlated highly significantly with both the empirical 50% thresholds (r_s = 0.631, $p < 0.001$) and the realised fraction of inferred states (r_s = -0.578, $p < 0.001$).

Author	clade	extinct	HER	T50%	SCG	Fchar	CG	Cdev	Euc	W	ESat	LSat
Anderson *et al*. 2011	Acanthodii	N	0.796	0.292	0.635	0.509	0.446	1.492	0.837	Top	N	Y
Sigurdsen & Bolt 2010	Amphibamidae	N	0.240	0.607	0.658	0.274	0.316	1.755	0.601	N	Y	Y
Hill *et al*. 2003	Ankylosauria	Y	0.377	0.209	0.585	0.712	0.687	6.010	0.750	N	Y	Y
Fröbisch 2007	Anomodontia	N	0.602	0.254	0.602	0.672	0.511	2.618	0.765	Top	N	Y
Hopkins 2008	Aplodontoidea	N	0.626	0.136	0.593	0.820	0.185	3.307	0.764	N	N	Y
Dupret *et al*. 2009	Arthrodira	N	0.565	0.147	0.571	0.774	0.566	3.425	0.715	Bot	N	N
Fortey & Chatteron 1988	Asaphina	Y	0.502	0.438	0.693	0.255	0.611	1.753	0.803	N	N	Y
Lieberman & Kloc 1997	Asteropyginae	Y	0.194	0.233	0.605	0.718	0.641	2.434	0.713	Top	N	Y
Alvarez *et al*. 1998	Athyridida	N	0.236	0.302	0.627	0.723	0.526	2.910	0.690	Top	N	Y
Milner *et al*. 2009	Baphetoidea	N	0.095	0.266	0.599	0.639	0.451	0.685	0.909	N	N	Y
Benedetto 2009	Billingsellidina	N	0.393	0.308	0.620	0.575	0.734	2.968	0.700	N	Y	N
Bodenbender & Fisher 2001	Blastoidea	N	0.311	0.153	0.588	0.834	0.609	4.058	0.662	Top	N	Y
Foote 1992	Blastozoans	Y	0.623	0.115	0.585	0.896	0.477	3.149	0.685	Top	N	Y
Wang *et al*. 1999	Borophaginae	N	0.710	0.447	0.645	0.344	0.502	1.690	0.698	Bot	Y	N
Gaffney *et al*. 2006	Bothremydidae	N	0.587	0.335	0.633	0.544	0.471	2.027	0.512	N	N	N
Schoch & Milner 2008	Branchiosauridae	N	0.532	0.301	0.601	0.593	0.269	1.752	0.792	N	Y	Y

Table 3.1 Summary metrics for the 93 clades in the dataset. Ext: N = does not terminate coincident with a mass extinction boundary; Y = does terminate coincident with a mass extinction boundary. HER: homoplasy excess ratio. T50%: 50% threshold for character states. SCG: Saturation CG. Fchar: fraction of total character states relative to the estimated maximum from Michaelis–Menten asymptotes. CG: Disparity profile centre of gravity. CDev: Summed centroid deviance. Euc: Maximum Euclidean distance between taxa in any given time bin as a fraction of the maximum across all time bins. W: Top, significantly top heavy; Bot, significantly bottom heavy; N, CG neither top nor bottom heavy. ESat: Y, disparity in the first two stages not significantly different from maximum; N, disparity in the first two stages significantly different from maximum. LSat: Y, disparity in the last two stages not significantly different from maximum; N, disparity in the last two stages significantly different from maximum. Clades that realize the maximum inter-taxon Euclidean distance are highlighted in italic.

Author	clade	extinct	HER	T50%	SCG	Fchar	CG	Cdev	Euc	W	ESat	LSat
Mihlbachler & Deméré 2010	Brontotheriidae	N	0.549	0.103	0.614	0.860	0.415	2.658	0.516	N	Y	N
Jimenez-Sanchez *et al*. 2010	Bryozoa (unnamed clade)	N	0.234	0.286	0.595	0.645	0.427	3.247	0.669	N	Y	N
Sampson *et al*. 2010	Chasmosaurinae	Y	0.665	0.283	0.612	0.604	0.458	0.644	0.533	Bot	N	Y
Smith & Zamora 2009	Cinctans	N	0.47	0.353	0.607	0.44	0.477	1.201	0.637	N	Y	Y
Carlson & Fitzgerald 2007	Cryptonelloidea	N	0.277	0.331	0.62	0.568	0.399	3.154	0.587	Bot	N	N
Novas *et al*. 2009	Deinonychosauria	Y	0.607	0.334	0.603	0.541	0.635	5.566	0.72	Top	N	N
Wenwei *et al*. 2006	Dimeropygidae	Y	0.539	0.371	0.61	0.551	0.528	0.722	0.697	N	Y	Y
Clement & Long 2010	Dipterimorpha	N	0.417	0.268	0.584	0.681	0.225	3.881	0.753	Bot	Y	N
Foote 1999	Disparida	N	0.276	0.146	0.575	0.803	0.49	2.82	0.506	Bot	Y	N
Cotton & Fortey 2005	Eodiscina	N	0.291	0.129	0.576	0.865	0.375	2.118	0.594	Bot	Y	N
Maletz *et al*. 2009	Eugraptoloida	N	0.861	0.26	0.631	0.567	0.563	2.093	0.646	N	N	Y
Bloch *et al*. 2007	Euprimateforms	N	0.416	0.358	0.594	0.613	0.348	2.897	0.623	Bot	Y	N
Tetlie & Cuggy 2007	Eurypterina	N	0.553	0.323	0.639	0.525	0.509	3.677	0.787	N	Y	Y
Foote 1999	Flexibilia	Y	0.339	0.213	0.612	0.755	0.506	2.855	0.493	N	N	Y
Zhu & Gai 2007	Galeaspida	N	0.659	0.279	0.582	0.601	0.549	4.357	0.729	N	Y	Y
Korn 1997	Goniatitaceae	N	0.737	0.5	0.628	0.27	0.569	3.519	0.866	N	N	N
Gebauer 2007	Gorgonopsia	Y	0.697	0.422	0.635	0.424	0.514	0.694	0.991	N	Y	Y
Prieto-Marquez 2010	Hadrosauroidea	Y	0.639	0.268	0.604	0.656	0.7	0.407	0.708	Top	N	N

Table 3.1 Summary metrics for the 93 clades in the dataset continued (1)

Author	clade	extinct	HER	T50%	SCG	Fchar	CG	Cdev	Euc	W	ESat	LSat
Wang 1994	Hesperocyoninae	N	0.636	0.481	0.704	0.404	0.52	3.467	0.668	N	N	Y
Polly 1996	Hyaenodontidae	N	0.454	0.37	0.622	0.501	0.54	1.627	0.797	N	N	Y
Motani 1999	Ichthyopterygia	N	0.699	0.372	0.614	0.415	0.359	5.625	0.77	Bot	Y	N
Trinajstic & Dennis-Bryan 2009	Incisoscutoidea	N	0.448	0.261	0.602	0.703	0.498	1.438	0.689	N	Y	Y
Sundberg 2004	Kochaspid Trilobites	N	0.122	0.313	0.65	0.561	0.485	1.225	0.66	N	Y	N
Adrain *et al*. 2008	Koneprusiinae	N	0.399	0.24	0.634	0.687	0.755	4.519	1	N	Y	Y
Klembara *et al*. 2010	Labyrinthodontia	N	0.301	0.214	0.576	0.706	0.368	2.492	0.658	N	N	N
Anderson *et al*. 2008	Lepospondyli	N	0.341	0.196	0.611	0.816	0.484	10.245	0.62	N	N	N
Pollitt *et al*. 2005	Lichoidea	Y	0.334	0.195	0.592	0.749	0.555	6.289	0.752	Bot	Y	N
Yates & Warren 2000	Limnarchia	N	0.344	0.224	0.599	0.741	0.437	4.957	0.64	N	Y	N
Hoffmann 2010	Lytoceratoidea	Y	0.835	0.5	0.655	0.428	0.468	2.287	1	Bot	Y	N
Damiani 2001	Mastodonsauroidea	N	0.342	0.302	0.575	0.533	0.394	2.592	0.726	Bot	Y	N
Young & De Andrade 2009	Metriorhynchoidea	N	0.869	0.332	0.639	0.489	0.451	5.418	0.78	N	N	N
Polly *et al*. 2006	Miacoidea	N	0.352	0.397	0.648	0.398	0.638	2.452	0.606	N	Y	Y
Ruta & Coates 2007	Microsauria	N	0.608	0.304	0.609	0.58	0.571	6.851	0.482	Bot	Y	Y
Lee *et al*. 2008	Missisquoiidae	N	0.096	0.214	0.598	0.742	0.379	2.828	0.761	N	N	Y
Bell Jr. & Polcyn 2005	Mosasauridae	Y	0.48	0.252	0.605	0.714	0.509	1.369	0.712	N	N	N
Kielan-Jaworowska & Hurum 2001	Multituberculata	N	0.465	0.31	0.628	0.54	0.52	3.535	0.774	Bot	Y	N
Pol *et al*. 2012	Notosuchia	N	0.435	0.353	0.621	0.482	0.355	3.968	0.5	N	N	Y

Table 3.1 Summary metrics for the 93 clades in the dataset continued (2)

Author	clade	extinct	HER	T50%	SCG	Fchar	CG	Cdev	Euc	W	ESat	LSat
Lieberman 2001	Olenellina	N	0.147	0.276	0.625	0.666	0.507	0.698	0.732	N	Y	N
Lieberman 1998	Olenelloidea	N	0.083	0.265	0.604	0.728	0.481	1.411	0.658	N	N	N
Bajpai *et al*. 2008	Omomyoidea	N	0.222	0.19	0.592	0.79	0.497	8.393	0.446	Top	N	N
McDonald *et al*. 2010	Ornithopoda	Y	0.691	0.176	0.598	0.764	0.62	1.076	0.992	Top	N	Y
Mitchell 1987	Orthograptidae	Y	1	0.529	0.645	0.067	0.628	1.338	0.626	N	Y	Y
Sansom 2009	Osteostraci	N	0.552	0.266	0.599	0.682	0.499	2.894	0.52	Top	N	N
Longrich *et al*. 2010	Pachycephalosauria	Y	0.48	0.442	0.625	0.469	0.631	1.791	0.655	Bot	N	N
Prokop & Ren 2007	Palaeodictyoptera	N	0.077	0.314	0.625	0.521	0.351	2.316	0.861	Bot	Y	N
Jin & Popov 2008	Parastrophinidae	N	0.414	0.321	0.612	0.652	0.118	4.577	0.565	N	Y	Y
Stocker 2010	Parasuchia	Y	0.374	0.329	0.618	0.489	0.496	0.369	0.761	N	Y	N
Lopez-Arbarello & Zavattieri 2008	Perleidiformes	Y	0.346	0.213	0.604	0.73	0.471	1.422	0.791	Top	Y	N
Smith & Pol 2007	Plateosauria	N	0.426	0.45	0.628	0.761	0.672	2.313	0.771	N	N	Y
Anderson *et al*. [81]	Placodermi	Y	0.638	0.271	0.584	0.528	0.56	2.515	0.65	N	N	N
Ketchum & Benson 2010	Plesiosauria	Y	0.375	0.264	0.606	0.709	0.509	3.684	0.762	N	Y	Y
Smith & Dyke 2008	Pliosauroidea	Y	0.616	0.274	0.596	0.693	0.506	3.001	0.743	N	Y	Y
Cisneros & Ruta 2010	Procolophonidae	Y	0.581	0.355	0.648	0.517	0.486	2.387	0.65	N	Y	Y
Huguet *et al*. 2002	Protomyrmeleontidae	Y	0.046	0.305	0.629	0.585	0.435	2.051	0.851	Bot	Y	N
Nel *et al*. 2005	Protanisoptera	N	0.478	0.313	0.576	0.563	0.451	1.732	0.949	N	Y	N
Egi *et al*. 2005	Proviverrinae	N	0.214	0.297	0.634	0.557	0.184	4.303	0.773	Top	Y	Y
Parker & Irmis 2006	Pseudopalatinae	Y	0.572	0.333	0.619	0.471	0.641	1.104	0.811	N	Y	Y
Pernègre & Elliott 2008	Pteraspidiformes	N	0.336	0.248	0.586	0.644	0.471	1.492	0.709	N	N	Y

Table 3.1 Summary metrics for the 93 clades in the dataset continued (3)

Author	clade	extinct	HER	T50%	SCG	Fchar	CG	Cdev	Euc	W	ESat	LSat
Lü *et al*. [153]	Pterosauria	Y	0.545	0.315	0.616	0.515	0.529	2.626	0.679	N	Y	N
Brusatte *et al*. 2010	Rauisuchia	N	0.517	0.388	0.619	0.501	0.508	3.31	0.753	N	N	N
Bates *et al*. 2005	Retiolitidae	N	0.578	0.333	0.623	0.517	0.557	2.765	0.704	N	N	N
Cerdeno 1995	Rhinocerotidae	N	0.327	0.131	0.586	0.831	0.517	2.379	0.772	N	Y	N
Hone & Benton 2008	Rhyncosauria	Y	0.764	0.411	0.587	0.365	0.568	2.877	0.88	N	Y	Y
Allain & Aquesbi 2008	Sauropoda	Y	0.538	0.38	0.606	0.478	0.539	3.85	0.774	Bot	Y	Y
Maidment 2010	Stegosauria	N	0.652	0.625	0.673	0.102	0.338	1.422	0.602	Bot	N	N
Carlson & Fitzgerald [101]	Stringocephaloidea	N	0.352	0.279	0.617	0.436	0.473	2.562	0.739	Bot	N	N
Schoch 2008	Stereospondyli	N	0.474	0.409	0.641	0.659	0.354	4.755	0.65	Bot	N	N
Lamsdell *et al*. 2010	Stylonurina	N	0.541	0.259	0.612	0.673	0.47	5.966	0.629	N	N	Y
Klug 2010	Synechodontiformes	N	0.641	0.288	0.627	0.645	0.617	1.561	0.2	Top	N	N
Gaudin 2004	Tardigrada	N	0.466	0.201	0.589	0.691	0.641	6.917	0.669	N	N	Y
Wu *et al*. 2009	Thalattosauria	Y	0.56	0.414	0.622	0.376	0.533	0.967	0.951	Top	N	N
Wilson & Märss 2009	Thelodonti	N	0.387	0.249	0.611	0.607	0.587	3.898	0.729	Top	Y	N
Hu *et al*. 2009	Theropoda	Y	0.422	0.3	0.611	0.567	0.579	2.125	0.971	N	N	N
Chatterton *et al*. 1998	Toernquistiidae	Y	0.141	0.308	0.593	0.593	0.462	0.793	0.653	Top	N	Y
Brusatte *et al*. 2010	Tyrannosauroidea	Y	0.778	0.372	0.645	0.405	0.633	3.267	0.95	Bot	N	N
Anderson & Seldon 1997	Xiphosura	N	0.896	0.575	0.59	0.076	0.266	4.934	0.803	Bot	N	N

Table 3.1 Summary metrics for the 93 clades in the dataset continued (4)

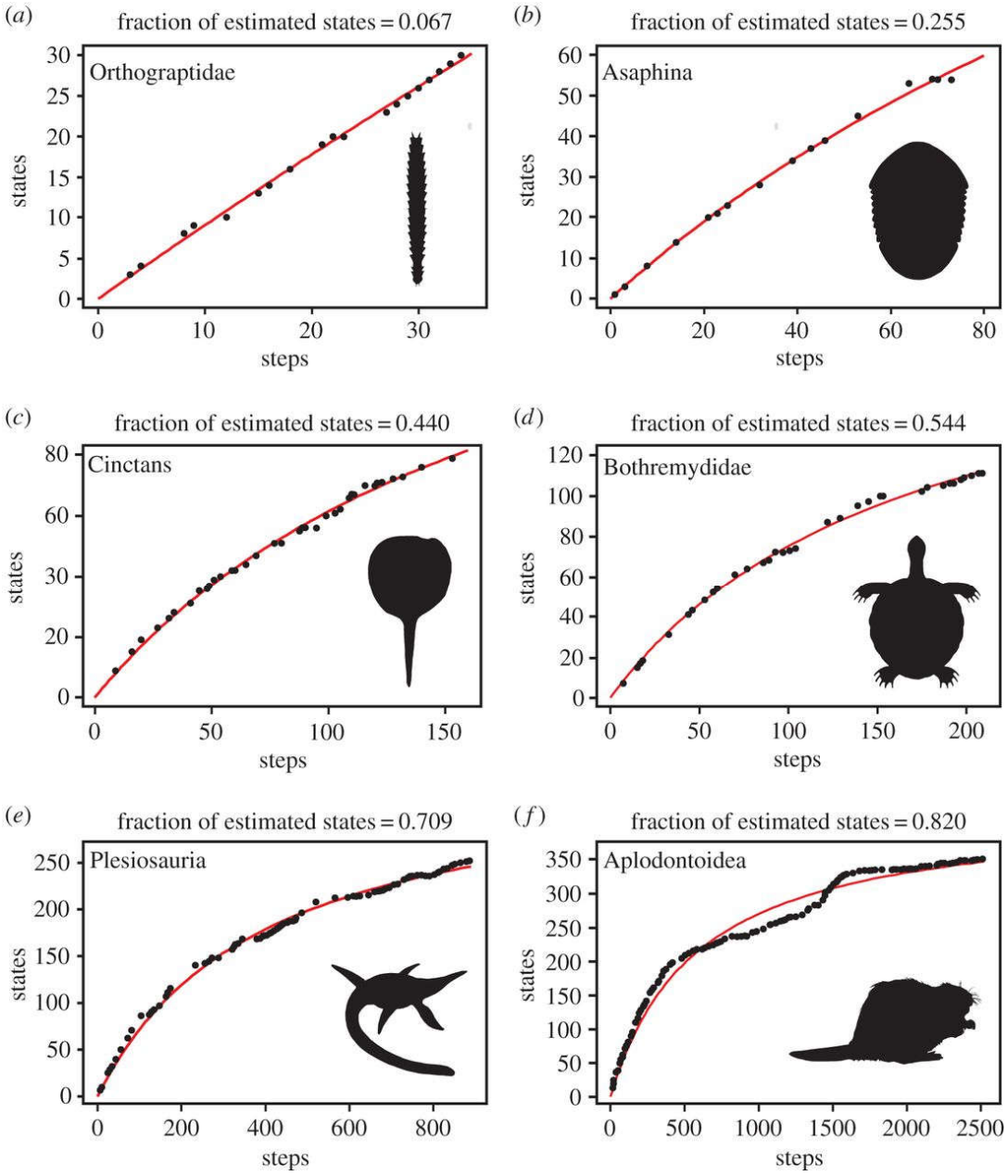


Fig. 3.3 Example Michaelis–Menten functions fitted to state/steps data for different extinct animal clades. See text for explanation of how the fraction of estimated maximum number of states was calculated. Points indicate cumulative totals as each branch is added. (a) Orthograptidae (Mitchell 1987). (b) Asaphina (Fortey & Chatteron 1988). (c) Cinctans (Smith & Zamora 2009). (d) Bothremydidae (Gaffney *et al.* 2006). (e) Plesiosauria (Ketchum & Benson 2010). (f) Aplodontoidea (Hopkins 2008).

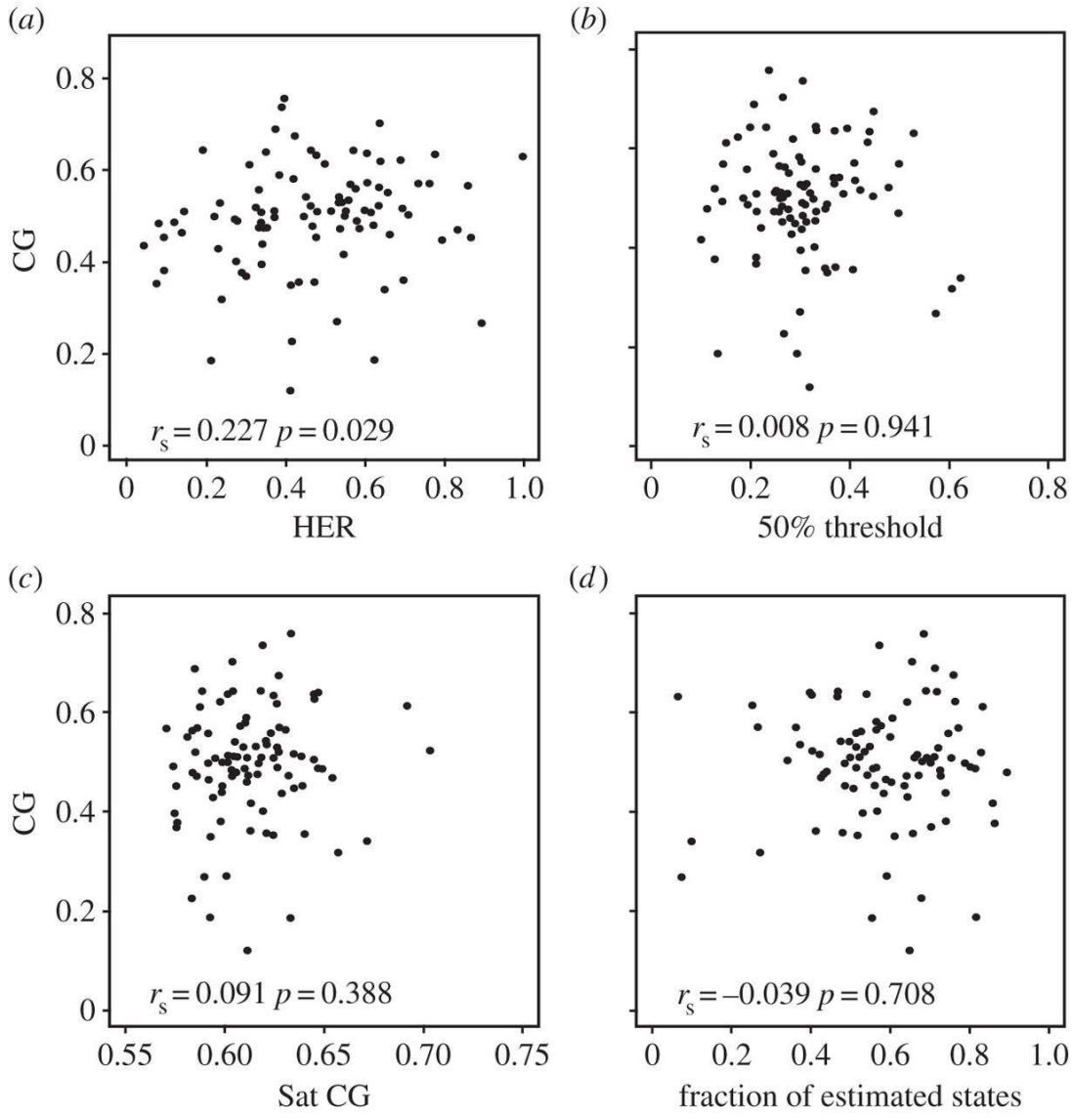


Fig. 3.4 Disparity profile centre of gravity (CG) plotted against homoplasy excess ratio (HER) and estimates of character saturation. (a) Disparity CG versus HER. (b) Disparity CG versus 50% threshold. (c) Disparity CG versus saturation curve CG. (d) Disparity CG versus fraction of the Michaelis-Menten estimate of the maximum number of character states realized at extinction. r_s and p-values are from Spearman's rank correlation coefficient tests.

There was a weak but significant negative correlation between overall homoplasy levels and the disparity CG (r_s = 0.227, p < 0.029): clades with a lower CG (earlier higher disparity) had greater homoplasy (lower HER) on average (**Fig. 3.4**).

However, we found no significant relationships between disparity CG and any of our indices of saturation curve shape (rs = 0.008, p = 0.941 for the 50% threshold; rs = 0.091, p = 0.388 for the saturation curve CG; rs = -0.039, p = 0.708 for the Michaelis-Menten estimate of the realised fraction of inferred states). Limiting the analysis to wholly extinct clades that did not terminate coincident with a mass extinction boundary resulted in weaker correlations for all indices of character saturation except the 50% threshold point (**Table 3.2**).

	HER	**50% threshold**	**saturation curve CG**	**observed maximum states/estimated maximum states**
disparity CG (entire dataset, *n* = 93)	r_s = 0.227 *p* = 0.029	r_s = 0.008 *p* = 0.941	r_s = 0.091 *p* = 0.388	r_s = 0.039 *p* = 0.708
disparity CG (clade extinction not coincident with mass extinction, *n* = 55)	r_s = 0.285 *p* = 0.035	r_s = −0.107 *p* = 0.436	r_s = 0.010 *p* = 0.940	r_s = 0.037 *p* = 0.786
disparity CG (clade extinction coincident with mass extinction *n* = 31)	r_s = 0.085 *p* = 0.649	r_s = 0.145 *p* = 0.438	r_s = 0.099 *p* = 0.597	r_s = 0.094 *p* = 0.614

Table 3.2 p-values from Spearman rank tests for homoplasy excess ratio (HER) and three proxies of character exhaustion (fraction of the total number of steps at which 50% of states are realized, CG of the saturation curve, and the fraction of the estimated number of states (inferred from Michaelis–Menten curve) that are observed) correlated with disparity profile CG. Values are calculated for the entire dataset of 93 clades, the subset of 55 clades not becoming extinct coincident with a mass extinction boundary and that have no extant survivors, and the subset of 31 clades that terminate at a mass extinction boundary.

Similarly, analysis of the CG of clades terminating at mass extinction boundaries yielded similar results for indices of character exhaustion but showed no correlation with HER values. Maximum Euclidean distance within a time bin correlated negatively with the Michaelis-Menten estimates of the realised fraction of inferred states (r_s = -0.228871 p = 0.027), indicating that character saturation may be greater in clades that reach their morphospatial bounds. However, no correlation was found between character saturation metrics and the amount of centroid deviation (50% threshold: r_s = -0.173, p= 0.097 saturation CG: r_s = -0.183, p=0.079 fraction of inferred states r_s= 0.198, p=0.057) implying that clades that migrate through the morphospace are as likely to show saturation as those that statically occupy a defined region. The morphospace of clades which show early disparity and similar saturation values (**Fig. 3.5**) reveals that some clades continue to evolve new character states as they migrate through the morphospace (eg. disparid crinoids) while others remain fixed and unoccupied space within existing bounds (eg. lichoid trilobites). Whether a clade showed early or late high disparity also had no effect on the degree of character exhaustion within that clade (**Table 3.3**).

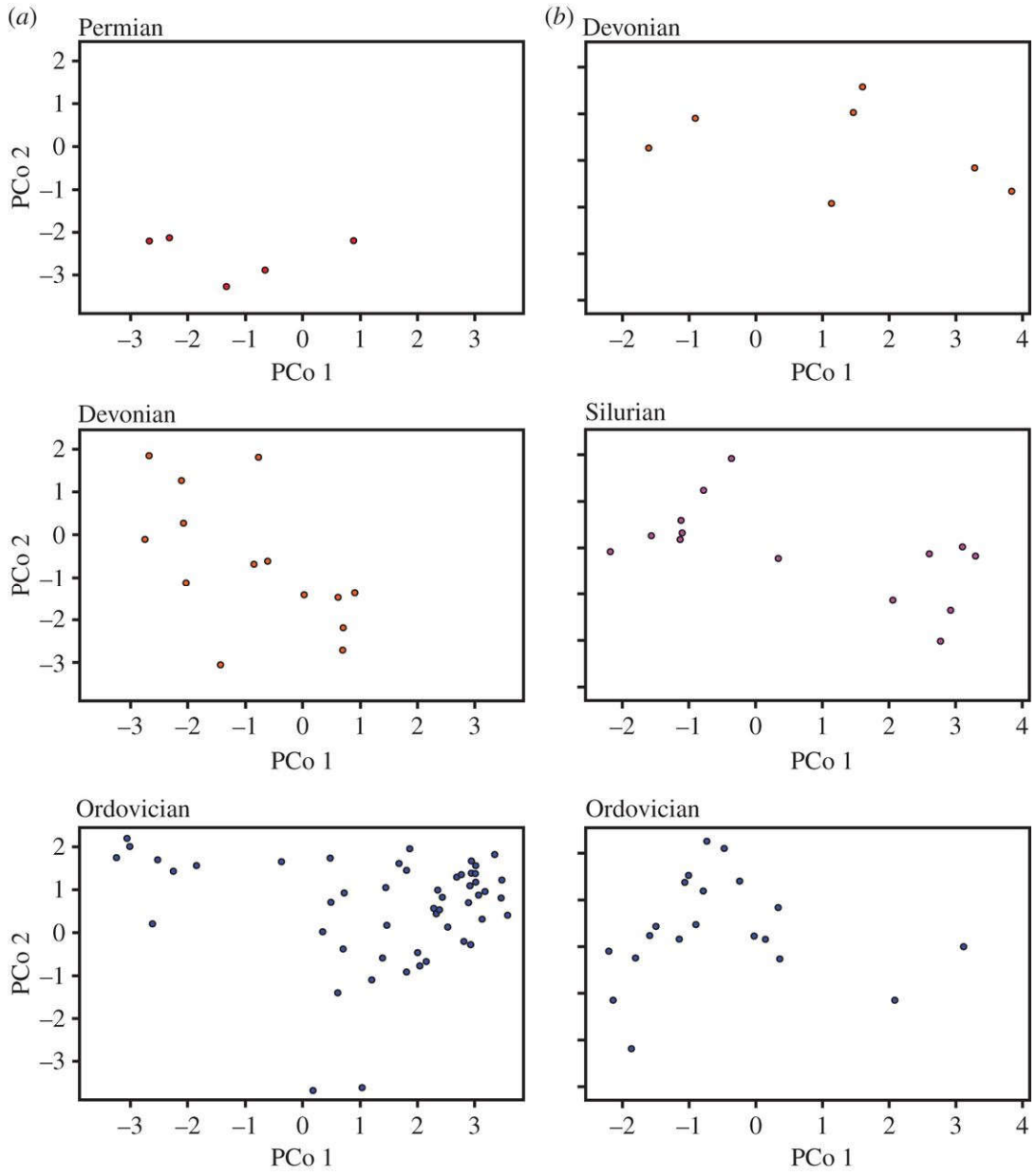


Fig. 3.5 Differing patterns of morphospace occupation along the first two principal coordinate axes in clades showing early high-disparity. CG: disparity profile centre of gravity. Fchar: fraction of total realized character states relative to the maximum estimated from Michaelis–Menten asymptotes. Euc: maximum Euclidean distance between taxa in any given time bin as a fraction of the maximum across all time bins. (a) Disparid crinoids from Foote 1999 (CG = 0.490, FChar = 0.803, Euc = 0.506) showing migration through the morphospace. PCo 1 = 23.6% total variance, PCo 2 = 12.0% total variance. (b) Lichoid trilobites from Pollitt et al. 2005 (CG = 0.555, FChar = 0.749, Euc = 0.752) showing more static occupation of the morphospace. PCo 1 = 26.2% total variance, PCo 2 = 13.4% total variance.

	HER	50% threshold	saturation curve CG	observed maximum states/estimated maximum states
significantly bottom heavy versus significantly top heavy	*W* =216 *p* =0.588	*W* = 288 *p* = 0.012	*W* = 219.5 *p* = 0.520	*W* = 110 *p* = 0.019
early maximum disparity	*W* =1277.5 *p* =0.131	*W* = 989 *p* = 0.482	*W* = 1077 *p* = 0.979	*W* = 1189.5 *p* = 0.407
late maximum disparity	*W* =997.5 *p* =0.535	*W* = 1095 *p* = 0.899	*W* = 1005.5 *p* = 0.580	*W* = 1051 *p* = 0.838

Table 3.3 Summary statistics from Mann–Whitney U tests of differences between median homoplasy excess ratio (HER) and three character saturation metrics (fraction of the total number of steps at which 50% of states are realized, CG of the saturation curve, and the fraction of the estimated number of states (inferred from Michaelis–Menten curve) that are observed) when bi-partitioned by disparity profile shape. Bottom heavy versus top heavy: clades grouped based on a CG value significantly higher or lower than mean randomized values (with other clades omitted). Early maximum disparity: clades partitioned according to whether or not they show disparity in the first two stages that is significantly different from the maximum. Late maximum disparity: clades partitioned according to whether or not they show disparity in the last two stages that is significantly different from the maximum.

4. Discussion

The significant but weak correlation between disparity CG and overall levels of homoplasy demonstrates that clades with higher disparity earlier in their histories are more likely to show higher levels of character state reversal and convergence. While this implies the operation of some constraint or restriction (*sensu* Wagner 2010), the small size of the effect (R^2 = 0.030 if modelled linearly) suggests that some other factor or factors are much more important. The absence of significant correlation between disparity CG and any of our proxies for states/steps curve shape indicates that disparity is not shaped in any straightforward way by progressive exhaustion of the character space. Patterns of disparity through time cannot therefore be deduced straightforwardly from patterns of homoplasy increase throughout the lifetime of clades, and are only weakly influenced by overall homoplasy levels. Many clades continue to evolve new character states with no associated increase in their disparity, while others achieve their highest levels of disparity through homoplastic character change. Several clades (including crustaceans and priapulid worms (Wills 1998a; Wills et al. 2012)) occupy a similarly sized morphospace envelope throughout much of their evolution (similar disparity), but nevertheless migrate through the overall morphospace. Other clades (e.g., angiosperms, Jurassic ammonoids (Gerber 2011)) quickly colonise many of the morpospatial extremes (reaching maximum disparity) but subdivide the envelope progressively through time and continue to evolve new states. The major axes of our empirical morphospaces are likely to be defined by the principal patterns of covariation between character states, and it is these patterns that largely determine Euclidean eccentricity from the global centroids. Similarly, the most eccentric morphologies may embody sets of character states that have individually evolved earlier in the history of the clade, but never before in combination. Upon its first evolution, a new state need not necessarily move a lineage to a particularly eccentric position in the morphospace, neither will it necessarily result in the expansion of the morphospace occupied by contemporaneous taxa, particularly where the space is contracting on other fronts.

In most of our sampled clades, new character states continued to evolve long after maximum disparity had been reached. Major groups often share a conserved morphological template or bodyplan (Bauplan), usually defined by character changes at the clade's base. This implies that some characters are relatively invariant or become 'fixed', while other characters continue to evolve new states. Neither conventional morphospace analyses nor our states/steps curves distinguished between characters on the basis of their evolutionary or developmental depth. State changes might therefore range from fundamental shifts in body symmetry and organisation (more typical of those delimiting phyla), down to subtle changes in bristle patterns at the other (perhaps more

typical of species), yet all contribute equally. To this extent, conventional discrete character morphospaces – and the estimates of disparity derived from them – may not be best suited for recognising the changes of deepest developmental and evolutionary significance. Morphospaces that take account of the developmental depth of characters have long been called for (Gould 1991), and some moves have been made towards realising these for particular clades (Brakefield 2008; Mitteroecker and Huttegger 2009; Gerber et al. 2011; Gerber 2014; Young et al. 2014) .

Several authors have distinguished between intrinsic and extrinsic limits to disparity (Hughes et al. 2013) , with intrinsic factors being those that operate within the individuals and lineages that constitute a clade (broadly equating to geometric and developmental constraints) and extrinsic or ecological factors being those imposed from the outside (biological and physical restrictions) (Erwin 2007; Wagner 2010) . The precise limits on the evolution of disparity are probably unique to each clade and comprise some combination of factors. Determining the relative importance of these is not straightforward, and direct tests are impossible with the present data. There are some strongly suggestive patterns, however.

4.1 Intrinsic developmental constraints

As ontogeny becomes more complex and genetic and other mechanisms become progressively more interdependent, increasing pleiotropy and functional linkage may result in developmental programs that are more difficult to modify and subsequently evolve (Anderson and Roopnarine 2005; Goswami and Polly 2010) . While some aspects of bodyplan organisation may be strongly adaptive and maintained by stabilising selection, other aspects may be largely contingent but locked down by the difficulty of effecting change in developmental programs. The seven cervical vertebrae of mammals furnish the best-known example. Nearly all mammals – including the long-necked giraffes, gerenuks and alpacas – have just seven neck vertebrae. Other vertebrate groups retain the ability to modify this number, and invariably evolve longer necks with greater numbers of vertebrae; up to 25 in birds, 19 in sauropods (Young and Zhao 1972) and 75 in the extinct plesiosaurs (Sachs et al. 2013). Two extant groups of mammals depart from the mammalian groundplan of seven; sloths have either six (*Choloepus*) or eight or nine (*Bradypus*), while manatees (*Trichechus*) have six. All achieve this by homeotic frame-shifts of the thoracic expression pattern (the development of ribs etc.) relative to the underlying somites (Varela-Lasheras et al. 2011). Such shifts in other mammals are accompanied by highly deleterious, pleiotropic side effects, not least problems with the innervation, musculature and blood-supply of the forelimbs and elevated rates of juvenile cancer (Galis 1999). Sloths and manatees appear to obviate

these effects by low rates of metabolism and overall activity (Galis 1999; Galis and Metz 2003; Galis and Metz 2007). The pentadactyl limb of tetrapods is another example of a design that was apparently much more labile early in its evolution. Early labrynthodont tetrapods had higher numbers of digits: eight in the forelimbs of *Acanthostega*, seven in the hindlimbs of *Ichthyostega*, six in *Tulerpeton*. Modern lissamphibians – despite their groundplan of five digits – often develop greater numbers with no ill effects: ostensibly because limb patterning in aquatic larvae occurs prior to the phylotypic stage of development, during which time inductive interactions and interdependencies are concentrated. Many amniote groups, by contrast, have reduced digit numbers as adults (e.g. horses, non-avian dinosaurs, birds (Salinas-Saavedra et al. 2014)), but few lineages have attained higher numbers, often evolving a variety of digit-like structures rather than extra digits *per se* (Galis et al. 2001; Mitgutsch et al. 2012). Ichthyosaurs furnish the best-known exception: opthalmosaurians added digits anterior to digit one and posterior to digit five (Wu et al. 2003), while non-opthalmosaurians may have achieved polydactyly by interdigital or postaxial phalangeal bifurcation (Motani 1999). In most amniote groups, however polydactyly is associated with a range of deleterious pleiotroipic effects (Alberch 1985; Quinonez and Innis 2014; Lande 2015), since limb development coincides with the phylotypic stage. Variation in this particular set of characters appears to be effectively locked down, therefore.

4.2 Extrinsic physical and biological (ecological) restrictions

In general, levels of clade disparity are often much less depleted by mass extinction events than levels of diversity. This is because numerous lineages can be lost from a morphospace whilst still maintaining a broad distribution of survivors (Villier and Korn 2004). Indeed, even where extinction selectively removes large subclades, disparity levels may remain high provided that the surviving clades are largely peripheral (Oyston, Hughes, Gerber, et al. 2015). Where increases in levels of disparity coincide with marked and episodic changes in the physical or biological environment, it may be reasonable to infer that extrinsic, ecological constraints have been removed. Such shifts may occur in the immediate wake of mass extinctions, although in such cases it may be difficult to distinguish the removal of biological constraints – for example, the extinction of competing or incumbent clades – from the physical environmental shifts that precipitate these biological changes. However, several of the largest and most conspicuous adaptive radiations have classically been understood in ecological terms. Crown group mammals evolved numerous new body forms (broadly equating to modern orders, and with many striking parallels between Eutheria and Metatheria in different settings) after the K/Pg mass extinction. This occured not only in the aftermath of the extinction of the non-avian dinosaurs, but also coincident with the final demise of eutriconodont,

spalacotheroid and multituberculate mammals (Luo 2007). Similarly, articulate brachiopods rapidly increased their disparity in the wake of the end Permian mass extinction; a pattern consistent with rebound after the removal of highly structured guilds and the freeing up of ecospace (Ciampaglio 2004). Comparable post-extinction rebounds have been observed for crinoid and blastozoan echinoderms (Ciampaglio et al. 2001), as well as ammonoids (Korn et al. 2013) through multiple events. Similarly rapid increases in disparity may occur when a clade is first able to colonise a fundamentally new region of ecospace. Even bodyplans that are assembled piecemeal over many tens of millions of years may reach a critical threshold, thereby suddenly circumventing previous restrictions (Brusatte et al. 2014).

5. Conclusions

In addition to studying the phylogeny and diversity of clades throughout their evolution (Gould et al. 1987; Foote 1997; Benton 2009), it is increasingly common to examine the manner in which groups explore theoretical or empirical morphospaces through time (McGhee 2006; Mitteroecker and Huttegger 2009), as well as their resulting temporal patterns of morphological disparity change. Disparity and diversity are fundamentally decoupled (Foote 1992), and a variety of trajectories have been observed empirically. The commonest pattern, however, is for disparity to peak relatively early in the history of a clade, and certainly before its peak in diversity (Hughes et al. 2013). Putative limits on disparity may either be intrinsic (e.g. developmental (Galis and Metz 2003; Gerber 2014)) or extrinsic (e.g. ecological (Ciampaglio et al. 2001; Ciampaglio 2004; Korn et al. 2013)), but both imply constraints and restrictions on available morphospace that might be reflected in the rate of evolution of novel morphology throughout the lifetime of a clade. The majority of clades studied do indeed show a significant decrease in the rate of appearance of novel character states over time. However, despite a weak correlation between overall levels of homoplasy (as measured by the HER) and the centre of gravity of clade disparity profiles (greater homoplasy implies earlier high disparity) we found no more detailed relationships between the shapes of character saturation curves and disparity profiles. Many clades continue to evolve new character states whilst disparity levels remain constant, which can variously be achieved by wholesale migration through the morphospace or by subdividing it. Similarly, disparity may be increased or maximized by predominantly homoplastic state changes. The anecdotally large number of clades showing the expansion of hitherto restricted morphospaces in the aftermath of mass extinctions (or upon transitioning into fundamentally new habitats) suggests that many of the limitations may be ecological. However, given the variation shown in both character saturation and morphospace occupation, limits on disparity almost certainly

result from a complex interplay of clade specific intrinsic and extrinsic factors, militating against a simple universal explanation for early high disparity.

Competing Interests

We have no competing interests.

Authors' Contributions

JWO wrote the paper, collected data, implemented analyses of homoplasy and character exhaustion and drafted figures. MH analysed disparity trajectories, collected data, wrote scripts and drafted figures. PJW scripted the states/steps analyses and wrote the paper. SG analysed disparity trajectories. MAW conceived the study, wrote the paper, analysed disparity trajectories and drafted figures.

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4 Which Source of Phylogenetic Information Is Most Congruent With Biogeographic Patterns?

4.1 Introduction

4.1.1 Chapter Summary

One of the most important consequences of the prevalence of convergent evolution is that it decreases the range of forms and traits seen in organisms and makes it more likely that the same character traits will arise on a tree independently. This phenomenon, known as homoplasy, is thought to be a major contributor towards phylogenetic error, particularly in morphological datasets. The perceived inaccuracy of morphological data is one of the factors which has contributed to the widespread adoption of molecular data, especially amino acid or nucleotide sequences. Although molecular techniques offer a number of advantages over morphological ones, they cannot be applied to the majority of organisms that have existed and quantitative, independent tests of the superior accuracy of molecular trees are almost non-existent. This chapter examines the use of biogeographic data to test support for morphological and molecular trees for the first time and compares it with another underutilised source of empirical data, stratigraphy. In a sample of 48 pairs of approximately contemporary morphological and molecular trees of animal and plant clades, molecular trees are significantly more congruent with biogeographical distribution patterns than their morphological counterparts. Results for stratigraphic data are more equivocal but also show greater support for molecular phylogenies. This finding has implications for the prevalence and structure of homoplasy in morphological data sets, the value of morphology as a check on molecular hypotheses, as well as the difficulties of analysing fossil groups for which molecular data are unavailable.

4.1.2 The Utility Of Phylogenetic Trees

Since the publication of the Origin of Species (Darwin 1859) evolutionary hypotheses have radically reshaped all aspects of Biology, most notably in ecology, taxonomy and medicine. This is largely due to applications of the comparative biological approach, looking for correlations in traits across different organisms. However, those organisms are nearly always non-independent datapoints, sharing an evolutionary history which

must be taken into account in order to make statistical comparisons valid (Harvey and Pagel 1991). Phylogenetic frameworks are frequently employed in parasitology (Page 1994; Monis 1999) and medicine (Gaunt et al. 2001; Abu-Asab et al. 2008; Weaver and Vasilakis 2009), as well as proving hugely important in the ecological study of traits (Edwards and Naeem 1993; Westoby et al. 1996), communities (Webb 2007; França et al. 2008), extinction (Nee et al. 1994; Cracraft 2001; Johnson et al. 2002; Andy Purvis et al. 2005; Purvis 2008) and conservation (Crandall et al. 2000; Andrew Purvis et al. 2005; Isaac et al. 2007). Needless to say, phylogenetic frameworks have also been instrumental in advancing our evolutionary understanding, particularly regarding both trait evolution (Dodd et al. 1999; Mooers et al. 1999; Wagner 2000; Oyston, Hughes, Wagner, et al. 2015; Mooers and Heard 2016) and macroevolutionary diversity patterns through time (Raup et al. 1973; Magallón and Castillo 2009; Jetz et al. 2012). Evolutionary trees are now so widely used that the quality of phylogenetic reconstructions directly impacts the ability to frame and test most hypotheses in biology (Lanyon 1993).

4.1.3 Methods Of Phylogenetic Inference

4.1.3.1 Early Morphological Techniques

Even before such attempts were explicitly linked to an evolutionary process, biologists have struggled with how best to infer the Tree of Life. In early attempts to infer phylogeny (Lamarck 1809; Gaudry 1866; Haeckel 1868; Tassy 2011) trees were derived from the distributions of morphological characters across species using a methodology with strong cultural and historical links to William Occam's principle of parsimony (Domingos 1999). After Darwin's Origin of Species a number of scientists, most famously Ernst Haeckel, continued to produce phylogenetic hypotheses (Haeckel 1866; Haeckel 1892; Haeckel 1894) which while theoretically informed by Darwin and Wallace's ideas, still used parsimony as the basis of largely qualitative judgements of evolutionary descent.

By the middle of the 20th Century, different schools of thought regarding how traits should be used in the field of quantitative phylogenetics created a range of different methodologies, most notably cladistics and phenetics (Mayr 1965). While the phenetic approach (Sokal and Sneath 1963) based on overall similarity proved popular initially it is generally considered to be a poor reflection of evolutionary relationships. It is therefore the advent of the cladistic methodology (Hennig 1950; Cain and Harrison 1960; Hennig 1966) coupled with fast, accessible computing methods (Farris 1970; Pankhurst 1991; Swofford 2003; Goloboff et al. 2003) that was largely responsible for standardising and popularising phylogenetic analyses in biology. Subsequently, morphology underpinned

most of our understanding of evolutionary relationships until the rise of fast and affordable sequencing technologies in the 1980s (Sanger et al. 1977; Smith et al. 1986; Prober et al. 1987; Clark et al. 2007).

4.1.3.2 The Rise Of Molecular Techniques

Since the turn of the century, molecular sequences and increasingly phylogenomic data have overtaken morphology as the preferred resource for phylogenetic inference. There are four practical reasons for this. Firstly, molecular data can now be acquired more easily and economically than morphological characters, the latter requiring painstaking comparative analysis and taxonomic expertise. In particular, modern DNA sequencing techniques allow vast amounts of nucleotide data to be generated and processed, with a complete knowledge of the genomes of several organisms now a reality (Venter et al. 2001; Clark et al. 2007; Hellsten et al. 2010; St John et al. 2012; Albertin et al. 2015). Secondly, morphological systematists must make judgements concerning the homology of their characters and the manner in which they are coded (Hawkins et al. 1997; Hawkins 2000). While subjective elements do exist in the analysis of molecular data (most notably when aligning sequences), automation and the application of repeatable rules mitigates some of this subjectivity. Thirdly, the direct equivalency of sequence data has led to well-established repositories for molecular data, and excellent protocols for their annotation. Published data can be easily curated, searched, repurposed and reanalysed alongside novel sequences. Despite ongoing concerted efforts to systematically archive morphological data sets and character descriptions, amalgamating morphological datasets often requires considerable manual effort, necessitating the interpolation and often recoding of characters. Fourthly, a well-developed body of theory and empirical data have given us a quantitative framework of how molecular evolution proceeds, allowing us to model this process in increasingly sophisticated ways. Most notably, it gives us the stochastic rate models key to clock and rate studies (Kumar 2005; Drummond et al. 2006). A similar framework does not yet exist for morphological evolution, with most analyses of morphological data based on parsimony, rather than probabilistic rate models. Although some recent efforts to apply Bayesian methods to morphological data have performed well in certain circumstances, the underlying models are still very much in their infancy.

4.1.4 Homoplasy In Morphological Data

In addition to these practical considerations, it has long been known that morphological similarity is not always indicative of evolutionary relationships (Boyden 1943). Ever since Richard Owen formalised the distinction between features which only appear similar (analogies) and features which share an identical structure and origin (homologies), how best to identify and use homologies to infer relationships has been much discussed in phylogenetic literature (Günter P Wagner 1989; Gunter P. Wagner 1989; Butler and Saidel 2000; Jones et al. 2009). It is generally agreed that robust tests of homology must assess both hypotheses of similarity due to anatomical or developmental similarities (primary homology) and hypotheses of a single origin in phylogenetic analyses (secondary homology) (de Pinna 1991). Incorrect homology assessments will therefore almost inevitably introduce homoplasy to phylogenetic analyses, which can lead to little agreement between topologies (Wake 1991), or even strongly support erroneous phylogenies as the result of incorrect assessments of secondary homology.

While homoplasy has been recognised and discussed for a long time, a surge in the recognition of convergence and more generally homoplasy in morphological data over the past 20 years led many to question its usefulness. Many of these arguments were spurred when molecular studies led to major phylogenetic revisions in some clades. In perhaps the most famous example our understanding of the phylogeny of mammals was almost entirely based on morphology since the 1950s (Simpson 1945; Shoshani and McKenna 1998), with little resolution of the relationships between major clades. The advent of multiple gene and phylogenomic data sets in the last decade has provided much greater resolution, as well as consistantly supporting some deep phylogenetic relationships (e.g. monophyletic Afrotheria) which are markedly at odds with prior morphological reconstructions (Jong 1998; Tabuce et al. 2008; Asher et al. 2009). Even more extreme, convergence and morphological plasticity in plants is so widespread that some have suggested that molecules should always have primacy (Scotland et al. 2003). In other cases, morphological and molecular data have contributed more iteratively to phylogenetic understanding. The deep phylogeny of arthropods is now fairly well constrained by molecular (and perhaps morphological) data to contain monophyletic Pancrustacea and Mandibulata groups (Regier et al. 2010). However, early multiple gene and phylogenomic analyses consistently supported the pairing of myriapods and chelicerates (Hwang et al. 2001): a clade (Paradoxapoda) so radically at odds with morphological data that it led to re-evaluation of molecular data, taxon sampling and analytical models. Recent thought has shifted to a more balanced approach, therefore, with morphological and molecular data often being used together or separately to support and test different phylogenetic hypotheses (Larson 1998; Wahlberg et al. 2005).

4.1.4 Limitations Of Molecular Phylogenetic Analyses

In many cases, molecular data has proved extremely useful in tackling cases where there is either a lack of resolution or outright conflict in phylogenetic studies based on morphology. DNA sequence data continues to prove useful in resolving problematic relationships within groups as diverse as reptiles (Wiens et al. 2010), birds (Prum et al. 2015) and insects (Yeates et al. 2012). While these molecular analyses can produce trees which are incongruent with existing morphological ones (Irestedt et al. 2004; Hirano et al. 2014; Covain et al. 2016) there are often good reasons to suppose that these estimates are more correct, especially when these new molecular hypotheses of evolutionary relationships are strongly supported by subsequent analyses.

Despite significant gains in the field of phylogenetics there are still many cases where inferring evolutionary relationships remains problematic even with access to increasingly powerful methods of sequence analysis. Firstly, different parts of the genome often have differing genealogical histories which do not reflect that of the whole organism (Degnan and Rosenberg 2006; Degnan and Rosenberg 2009) and it is fairly common to have molecular incongruence where multiple conflicting molecular phylogenies exist. Secondly, the limited number of possible character states at any given site makes it possible for base-compositional similarities to arise convergently in high enough frequencies to overwhelm historical signal (Naylor and Brown 1992). This loss of phylogenetic information resulting from substitution saturation is recognised as one of the biggest difficulties in generating accurate molecular phylogenies (Lopez et al. 1999; Xia et al. 2003). Attempts to solve these problems have focused primarily on analysing larger samples of sequences from multiple genes, with the hope that the consensus reflects the true pattern of descent and will, therefore, allow us to filter out the ‘noise’ of homoplasy from the genuine phylogenetic signal. While this may work in some cases (Philippe et al. 2005), evidence suggests that in others simply analysing more data does not reduce phylogenetic conflict (Philippe et al. 2011).

An even greater problem is that our only record of most of evolutionary history comes from the fossil record where highly incomplete morphological data is all we have with which to infer relationships (Donoghue et al. 1989). Discounting such taxa both dramatically impairs our ability to study long term evolutionary trends (Slater et al. 2012) and is known to result in less well resolved phylogenies (Huelsenbeck 1991). The disagreement in and limited availability of molecular data make it essential to incorporate other independent sources of data with which we can infer support for our phylogenetic trees, especially given widespread morphological convergence and homoplasy. This independent data is primarily of two kinds: stratigraphic and biogeographic, which are discussed below.

4.1.5 Stratigraphic Data & Phylogeny

Phylogenies of both extant and extinct groups are often evaluated with regards to fossil age ranges, with numerous authors arguing that phylogenetic and stratigraphic data are independent (Gauthier et al. 1988; Norell 1992; Norell and Novacek 1992; Benton 1995b; Benton and Hitchin 1996; Benton and Hitchin 1997). If the fossil record is complete, then every morphological change would be represented by fossils in a perfect chronological sequence. The correct phylogeny would be the one with branching patterns of morphological change which perfectly match this sequence. In reality, the incompleteness of the fossil record is likely to cause some traits to appear out of sequence. Studies of tetrapods (Maxwell and Benton 1990) and the marine fossil record (Sepkoski 1993) suggest that the overall patterns of diversification have remained relatively unchanged since 1900. It, therefore, seems likely that the stratigraphic history of groups with a relatively good hard part fossil record is likely to be a reliable and independent indicator of evolutionary history or, at least, all records are affected by common biases to similar extent (Benton et al. 2000).

In order to evaluate congruence between stratigraphy and phylogeny quantitatively, several different indices have been developed. Most notable among these is the Spearman rank correlation (SRC) (Gauthier et al. 1988), the stratigraphic consistency index (SCI) (Huelsenbeck 1994), the relative completeness index (RCI) (Benton 1994; Benton and Storrs 1996) and the gap excess ratio (GER) (Wills 1999). The SRC test simply compares the order of points and doesn't account for spacing in time or degree of mismatch. While early studies gave significant results for around half of the clades studied (Norell and Novacek 1992; Benton and Storrs 1996), that proportion fell significantly with subsequent assessments of tetrapods, fishes and echinoderms (Benton and Hitchin 1996; Benton and Hitchin 1997). Both the RCI and SCI metrics seem to perform better, with over 50% of example clades within each group showing significant correlation (Benton and Hitchin 1996; Benton and Hitchin 1997). Both RCI and SCI values are affected by the tree balance and stratigraphic ranges of the datasets being analysed, skewing comparisons between trees of different shapes and taxon compositions (Siddall 1997). While the SCI uses taxon first occurrences to evaluate the proportion of consistent nodes, the RCI combines a measure of the extent of ghost ranges with the extent of combined ranges. This means it is well suited to assessing the quality of a group's record, but also that it is not a pure index of the congruence of the tree with the order of appearance of fossil groups. The gap excess ratio expresses the proportion of the total ghost range necessitated by the constraints of the tree (Wills 1999) and, therefore, provides better estimates of stratigraphic congruence. This metric was later modified to take into account differences in tree balance (Wills et al. 2008). This

modified gap excess ratio metric found exceptional levels of congruence between phylogenetic and stratigraphic data for major dinosaur clades, implying that both phylogenetic and stratigraphic data accurately represent the evolutionary history of dinosaurs.

Although a number of studies demonstrate high congruence between stratigraphy and phylogeny, whether stratigraphy consistently supports more accurate or even particular types of tree has received very little study. Tests on a sample of 206 mammalian cladograms using 3 indices of stratigraphic fit (SRC, SCI and RCI) were inconclusive, showing that while SRC and SCI favour morphological trees, RCI shows slightly greater congruence with molecular phylogenies (Benton 1998). There has, until now, been no such evaluation of other measures of stratigraphic fit, such as GER*. Testing the reliability of phylogenies using stratigraphy is also dependent on the amount of fossil material available. Fewer first and last occurrences will make stratigraphic data more congruent with a greater range of trees, making tests of stratigraphic congruence of limited use for evaluation evolutionary trees for groups with poor fossil records. Finally, as fossil taxa are defined primarily through the identification of shared morphological characters these stratigraphic assessments are, to some extent, subject to the same biases affecting morphological data and so might, in some cases, provide false support for morphological trees.

4.1.6 Biogeographic Data & Phylogeny

As tests of stratigraphic congruence may be biased or of limited power in some cases, it is imperative we utilise other independent methods of testing phylogenies where possible. Observations that the distributional patterns of species were, to some extent, linked to their evolutionary history played a key role in developing the theory of evolution through natural selection (Camerini 1993), although the process by which this occurs is less clear. While most early workers focused on ancestral range expansions, dispersal and subsequent reproductive isolation (Wallace 1876) the later vicariance school proposed that most biodiversity was generated as the result of the fragmentation and geographical isolation of ancestral populations (Nelson and Platnick 1981). Modern biogeographic theory recognises the importance of both of these processes, although their relative importance is still hotly debated (Zink et al. 2000). Especially contentious is the idea that long-distance dispersal may be more common than previously thought, reducing the importance of geographic barriers which have long been assumed to effectively isolate populations (Gillespie et al. 2012).

The rejection of vicariant mechanisms in many cases has seen the school of thought within the biogeographic field shift away from historical contingency and long-term evolutionary processes in favour of ecological factors such as environmental tolerance and competition (Rey Benayas and Scheiner 2002; Frainer et al. 2017). However, some of the preference for ecological mechanisms seems to be based largely on the ability of environmental variables to fit the data (correlation) and a-priori reasoning, with many studies failing to test for historical contingency at all (Warren et al. 2014). Studies of island radiations often show strong historical evolutionary patterns, from Darwin's classic work on island radiations in the Galapagos on tortoises and finches (Caccone et al. 2002; Grant and Grant 2011) to more recent genetic studies of island clades, most notably in Hawaiian silverswords and spiders (Baldwin 1997; Gillespie 2004). These patterns are so striking and prevalent that island biogeography has developed into a field in its own right (Macarthur and Wilson 1967) with a range of applications in non-island systems at a range of scales (Patterson 1999; Jacquet et al. 2017; Pinheiro et al. 2017).

Furthermore, parallel radiations into the same range of niches in isolated regions can often produce convergent morphologies that are responsible for at least some of the incongruences between morphological and molecular trees. Striking examples of convergence are well known from island radiations of Caribbean anoles (Losos et al. 1998) and Hawaiian lobeliads (Givnish et al. 2009). A similar history of geographic isolation seems to be responsible for the spectacular extent of convergence in the adaptive radiations of cichlid fish in East African lakes (Kocher et al. 1993; Winemiller et al. 1995; Muschick et al. 2012) and ranid frogs (Bossuyt and Milinkovitch 2000) in Madagascar and India. Similar patterns can be found on a grander scale in the fossil record, such as widespread functional convergence in the eutherian mammals of Europe and North America and the metatherian mammals of Australasia and South America (Nevo 1979; Goswami et al. 2011). The science of phylogeography (Avise et al. 1987; Bermingham and Moritz 1998) in particular has used molecular data to great effect to investigate the links between phylogeny and species distribution in numerous clades (Taberlet et al. 1998; Tolley et al. 2006; Meredith et al. 2011). In several of these cases, phylogenetic revisions from molecular data have proved key in illuminating these convergent radiations. Perhaps the best known example of this is the phylogeny of living placental mammals. Analyses of various nuclear and mitochondrial genes strongly support the monophyletic Afrotherian and Laurasiatherian clades (Murphy, Eizirik, O'Brien, et al. 2001; Wildman and Uddin 2007; Asher et al. 2009), a result also supported by rare genomic changes (Madsen et al. 2001) and recent fossil material (Tabuce et al. 2007). While the groups may have originated elsewhere, both Laurasiatheria and the largely endemic Afrotheria demonstrate that there are significant levels of biogeographic congruence in the placental mammal phylogeny. While case studies of other mammalian

and bird clades show a similar signal (Teeling et al. 2005; Rowe et al. 2008; Claramunt and Cracraft 2015) but it has not yet been tested whether molecular phylogenies consistently show higher congruence with present biogeographic patterns than their morphological counterparts. If the pattern seen in placental mammals is a general rule rather than an exception, it would suggest that biogeographic data may be useful as an independent data source to test competing phylogenetic hypotheses.

4.1.7 Aims

Although the argument for the primacy of molecular data over morphology is usually assumed to be settled this has never been empirically tested. This chapter assesses the relative quality of morphological and molecular trees for two reasons. Firstly, it is impossible to acquire molecular data for most extinct and fossil groups and morphology, therefore, offers the only means to resolve their phylogeny. Secondly, trees derived from different molecular datasets can still show significant disagreement, making it unclear which topology is the most accurate. Morphology is still the most used source of phylogenetic information for many groups of organisms and although tests of phylogeny against a group's stratigraphic record are somewhat common there has, to date, been no similar test of biogeographic congruence.

This chapter will examine the use of biogeographic and stratigraphic data to support phylogenies by addressing the following aims:

i) Identifying and compiling pairs of morphological and molecular phylogenies for a diverse range of largely extand animal and plant clades from the existing phylogenetic literature, taking steps to ensure the trees are as comparable as possible.
ii) Develop a method of codifying biogeographic distributional data for extant terminal taxa in these clades in a manner that is amenable for phylogenetic congruence tests.
iii) Develop suitable metrics and quantitative methods to assess the general congruence of phylogenies with biogeographic distributions, specifically whether biogeographic congruence is greater than expected by chance.
iv) Assess whether biogeographic distributions are consistently more congruent with either morphological or molecular trees.
v) Assess stratigraphic congruence in a subset of clades with sufficient available fossil data for terminal taxa using a wide range of metrics, including GER and GER* to determine whether stratigraphic congruence and biogeographic congruence tend to agree in the phylogenies they support.

4.2 Methods

4.2.1 Sample Collection & Treatment of Phylogenies

Published phylogenies for a range of clades were portioned into two categories: morphological or molecular, taken from 36 years of phylogenetic literature dating from 1980 to 2016. Searches were conducted using Google Scholar primarily, but also Web of Science, using clade names as search terms. The search was limited to clades which were known to have or were likely to have different distributions and unambiguous ranges (marine clades and migratory clades were largely omitted for this reason). Source papers which presented both morphological and molecular trees were used as these tend to have identical taxon sets and sampling procedures for each phylogeny, making them directly comparable. Datasets were classed as morphological if they did not include any DNA, RNA, carbohydrate or protein data, regardless of whether such characters were soft part, hard part or physiological. Similarly, datasets were classed as molecular if they contained only DNA, RNA, carbohydrate or protein data. No distinction was made between different sources of molecular data, although the majority of molecular datasets consisted of DNA sequence data incorporating multiple genes. Of the trees obtained, the majority (77 out of 90) were constructed under parsimony, with 10 maximum liklihood and 5 Bayesian trees in the molecular partition. A very small minority of trees were constructed using other methods, with 3 morphological trees and 1 molecular tree being a consensus of previous phylogenetic studies and 1 morphological UPGMA tree. Phylogenies were preferentially taken from the main text of the paper, with supplementary material only being used if there were no suitable tree figures in the main text. In some cases, for example, a paper might present a combined analysis of all data, with separate morphological and molecular topologies as supplementary materials. In some cases, multiple phylogenies of a given category were presented in the main paper or as supplementary information, in which case the one preferred by the authors was used (either on grounds of analytical rigor on inclusivity of data). In cases where no preference was expressed, the most inclusive (in terms of taxa, then in terms of characters) was used. Finally, in the event that all possible candidate trees contained exactly the same number of taxa and characters, the most resolved topologies were used. In order to control for the size and nature of the taxon sample, the minimum number of leaves were pruned from one or both trees in order to make the leaf sets identical. This was done primarily to collapse trees down to the same resolution when one topology had greater resolution than the other, but was also used to remove some taxa not present in both phylogenies. The percentage of taxa removed from source matrices was relatively low (11% for morphological datasets and 22% for molecular data)

and the majority of clades had their full original taxon set (70% of morphological datasets, 66% of molecular).

4.2.2 Characterising Biogeographic Regions

Biogeographic data were obtained from The IUCN Red List of Threatened Species, Version 2017-2 (IUCN 2014), the Global Biodiversity Information Facility (GBIF: The Global Biodiversity Information Facility 2016) and The Reptile Database (Uetz 2012). In order to ensure this information was as up to date and accurate as possible, these data were checked and augmented using literature searches conducted on Google Scholar with leaf taxon names, 'biogeography' and 'distribution' as keywords. The regions in which taxa are present were compiled for each leaf to produce a summary range map for the clade. This range map was then used to produce a data matrix of leaf presence/absence within each region (**Fig. 4.1**).

Data were initially collated as presence/absence for the areas listed in the original database (which were usually islands or districts/regions within a country) rather than using latitude and longitude for the individual datapoints. This is because the collection of occurrence data is usually unevenly distributed, with vastly greater sampling in areas near populated areas (large cities being the prime example) and almost no sampling in relatively inaccessible areas (e.g. mountainous regions, forests and remote islands). Therefore just using raw point occurrences, despite seeming better resolved, is more likely to give erroneous representations of distribution. Taxa were scored with a 1 if present and a 0 if absent for the smallest regions listed. If the regions listed were at different scales for different taxa (e.g. districts for some, countries for others), the larger region was broken up into its constituent sub regions to match the finest scale given, with taxa coded as present for the larger region coded as present for all new regions within it. For example, if one taxon was listed as occurring in 'North America' but several other taxa had distributions listed as being limited to specific states, the 'North American' taxon would be recorded as occurring in all of the states harbouring the other taxa. This helped to ensure all regions for a clade were summaries of biogeographic distribution at the same scale. Regions were then checked to ensure none of them overlapped or were duplicates of the same area to produce a full list of the least inclusive regions in which the members of the clade were found. The list for each taxon was converted into a single matrix for the clade in which presence in a region was encoded by 1s and absences by 0s.

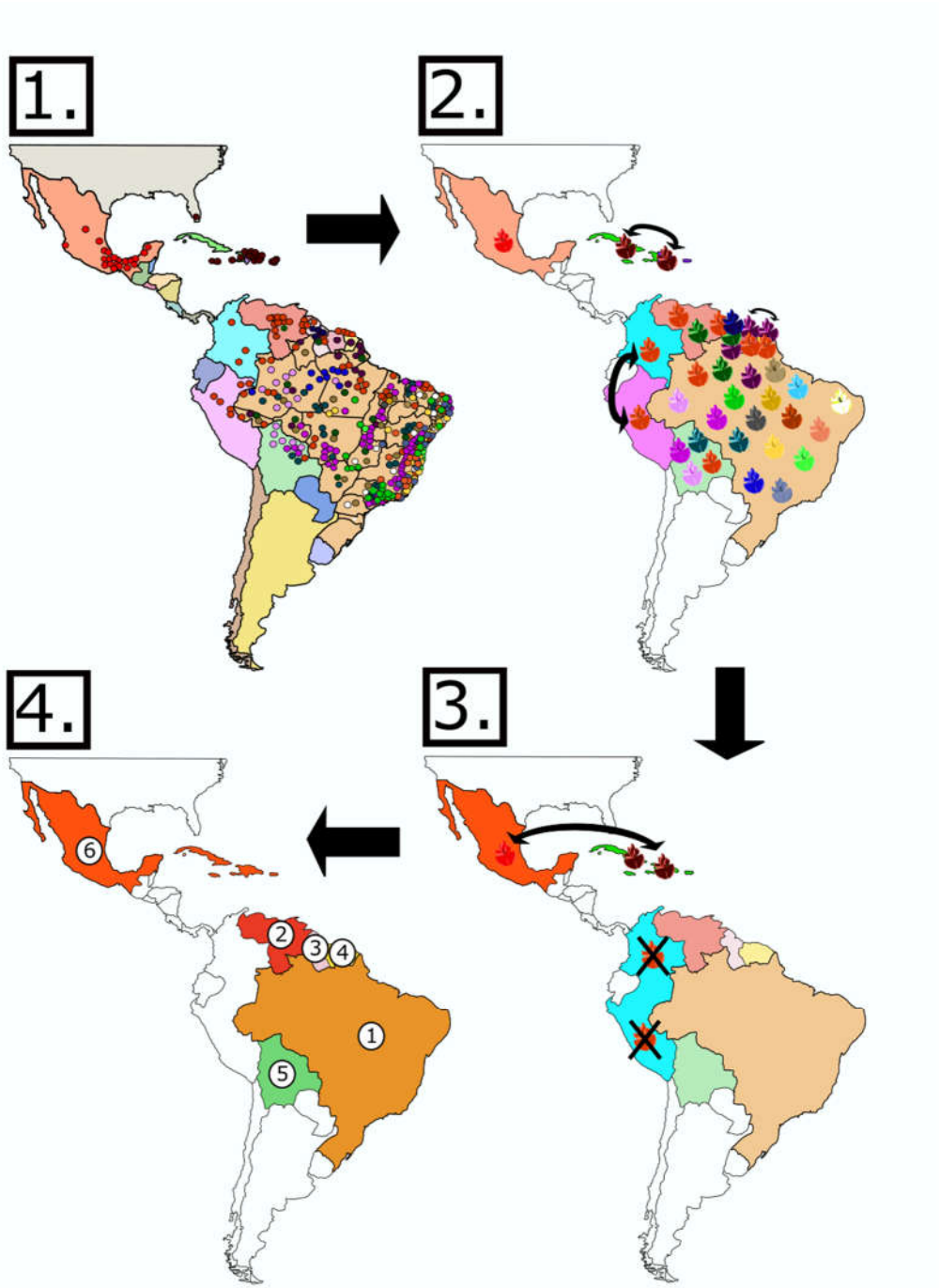

Fig. 4.1 Characterising Biogeographic Regions. Taxa are of the flowering plant genus *Andira*, with occurrence data taken from GBIF. **1.** Occurrence data is collected for each taxon in the clade being analysed from online repositories (GBIF, IUCN Redlist). Different coloured points represent different taxa, the delineated coloured areas are countries**. 2.** The occurrence data is used to codify taxon presence/absences in each geographical unit (countries in this case). Coloured areas are countries containing taxa, with taxon presence shown by coloured symbols. Arrows indicate adjacent countries with identical taxon sets**. 3.** Adjacent countries with identical taxa are combined into new regions. Both Mexico (orange) and the Caribbean (green) have only endemic taxa and will be combined (geographically closest) while the Colombia+Peru region (light blue) has only one taxon which it shares with other regions and so will be removed. **4.** Final numbered regions with unique taxon compositions.

A number of steps were taken to reduce region matrices down and eliminate redundant or duplicate information. Firstly, regions with identical taxon codings (i.e. the same leaf set was present in both regions) were combined, defining a new set of regions with unique presence/absence codings. By this process, adjacent regions with identical codings were combined into a single larger region until all regions were adjacent to regions with different taxon compliments. Although duplicate regions or regions with the same presence/absence codings strengthen the associations between certain taxa in the matrix they are not biogeographically distinct (unlike regions with unique taxon compositions) and so were amalgamated. Conversely, automorphic characters serve no role in determining the fit of region characters onto phylogenies. As our region characters serve only to identify groupings of taxa with overlapping or proximal distributions, these autapomorphic region characters serve no purpose. The second step, therefore, involved removing all regions containing only a single taxon. In cases where this would result in a taxon being removed from the matrix the region was instead combined with the closest neighbouring region, choosing the region with the fewest taxa in the case of ties. This ensured that all automorphic characters were removed from the matrix while still retaining distributional data on all taxa in the clade. Finally, the list of biogeographic regions was checked to ensure that they were broadly comparable in terms of biogeographical separation (for example continents or island archipelagos, neighbouring islands in a chain). For clades with a global distribution this approach typically resulted in biogeographic regions broadly congruent with the modified version of Wallace's biogeographic regions (Holt et al. 2013).

4.2.3 Quantifying Dataset Properties

Source trees differed considerably in their size (number of leaves), balance, taxonomic scope, biogeographic range and the number of regions distinguished. All of these might be expected to influence or bias potential statistics for the goodness of fit of the biogeographical data to the tree. However, all except tree balance were controlled in our sample of morphological and molecular tree pairs. Nevertheless, these variables were summarised. Heard's index of tree imbalance (Im) was calculated using the GHOSTS 2.4 script (O'Connor and Wills 2016). This index tallies the number of terminal taxa subtended by the right hand (T_R) and left hand (T_L) branches at each internal node, then scales this value by a function of the number of taxa in the tree (n):

$$Im = \frac{\sum T_R - T_L}{(n-1)(n-2)/2}$$

Index values of 0 reflect a perfectly balanced tree, with values increasing as the topology becomes more imbalanced up to a value of 1 for a completely pectinate tree.

4.2.4 Measures Of Biogeographic Fit

4.2.4.1 Consistency Index

Biogeographical congruence for each clade was evaluated by parsimoniously optimizing the corresponding biogeographical matrix onto both morphological and molecular trees using PAUP* 4.0 (Swofford 2003) . The following metrics were recorded. The ensemble consistency index (CI) (Kluge and Farris 1969) is given by the minimum possible number of state changes (the total number of states in the matrix, minus the number of characters) divided by the number of observed state changes on the tree. A 1:1 correspondence of phylogeny and biogeography (i.e. all regions correspond to monophyletic clades) results in a CI of 1.0.

$$CI = \frac{MinSteps}{ObsSteps}$$

It is well recorded (Sanderson and Donoghue 1989) that the CI is negatively correlated with the number of taxa in the dataset and to a lesser degree the number of characters (Archie 1989) . This means that comparisons of CI values are only really valid for trees derived from the same data (that is, they are the same length). However, in the study both the taxon set and the region characters were identical for the morphological and molecular trees being compared, with only the tree topologies differing. Therefore, neither of these factors should bias comparisons made in this study.

4.2.4.2 Retention Index

The retention index (RI) is an index of retained synapomorphy (shared, derived states), and is less sensitive to both the number of taxa and the number of characters in a dataset. The RI is the maximum number of possible steps minus the observed number of steps divided by the maximum number of possible steps minus the minimum number of steps. An RI of 1 means the character set fits onto the tree perfectly, an RI of 0 means the character set fits the tree as poorly as possible.

$$RI = \frac{MaxSteps - ObsSteps}{MaxSteps - MinSteps}$$

The RI is still sensitive to the number of states per character, with values becoming increasingly inflated as the number of character states increases (Naylor and Kraus 1995). As the number of character states increases, the number of taxa that share the same state decreases. States shared by fewer taxa have fewer homoplastic

configurations, resulting in increasingly inflated RI values with more unique character states.

4.2.4.3. Biogeographic Homoplasy Excess Ratio

The homoplasy excess ratio (HER) (Archie 1989; Farris 1989; Archie 1990; Archie 1996), was designed to overcome these biases in CI (and to a much lesser extent the RI) caused by the differences in the dimensions of datasets, particularly the anticipated increase in homoplasy with increasing numbers of taxa. HER is given by the observed homoplasy excess (the number of steps observed on the minimum-length tree minus the minimum possible number of steps) divided by the maximum homoplasy excess (the mean number of steps for minimum-length trees for randomised data, minus the minimum possible number). In the original implementation of the index, data are randomised by reassigning states across taxa but within each character. This breaks down character correlations and the internested structure necessary to infer phylogeny. Hence:

$$HER = 1.0 - \frac{ObsSteps - MinSteps}{MeanSteps - MinSteps}$$

The ratio of the observed homoplasy excess/maximum homoplasy excess is subtracted from 1.0 so that the HER will be 1.0 when no homoplasy is present. Completely phylogenetically random data has an expected HER of 0.0.

We modified this procedure here in two ways. Firstly, we treated the biogeographical data as a single column, randomly reassigning these to rows, such that species nominally retained their patterns of biogeographical distribution. Secondly, rather than infer an optimal tree or trees from these reassignments (which would, in any case, be identical to the original), we optimised the biogeographical characters onto the original tree (effectively randomising the assignment of species and their biogeographical distributions across the same topological branching structure.

4.2.4.4 Significance Values For CI & RI

Randomisation tests were conducted to determine whether the values we observed were greater than those expected for the particular topology and dataset. As outlined above, the HER already scales its measure of homoplasy relative to the maximum amount of homoplasy expected given the data and tree, while calculation of both the CI and RI makes no such consideration. Therefore, we randomly reassigned each taxon's block of region character codings 10,000 times to produce 10,000 randomised matrices. CI and RI was calculated for each randomisation to produce distributions of expected CI and RI

values. Observed CI and RI values were then compared to these distributions. Observed values that fall beyond the 95th percentile (i.e. greater than or less than 95% of random values) were taken to show biogeographic congruence which is statistically significant from that expected by chance. HER instead accounts for this distribution of expected values implicitly, as the mean and minimum possible number of steps (tree length) is factored in during the calculation. Therefore, statistical tests of HER used the raw values for the whole dataset.

4.2.5 Testing For Dataset Biases

Before further statistical analyses, Shapiro-Wilks tests for normality were performed. The majority of data partitions were non-normally distributed and as a result, all subsequent statistical tests were non-parametric. In order to test the effect of different dataset properties on our fit metrics, a number of nested linear models were fitted with each fit metric as the dependent variable. Model fit was then evaluated using the Akaike information criterion (AIC). Both year of publication and the number of phylogenetic characters used to construct the trees indirectly represent an improvement in phylogenetic information and could therefore conceivably impact our measures of biogeographic congruence. In order to investigate this each metric was plotted against the number of phylogenetic characters and publication year. Due to the data being non-normally distributed and showing unevenly distributed residuals (high heteroscedasticity), the Spearman-rank correlation co-efficient was used to assess correlation between variables for the whole dataset. A few of the datasets showed numbers of phylogenetic characters which were substantially larger than the rest, so a separate analysis using Pearson's correlation coefficient was used to assess correlations on a subset of the data with outliers removed.

4.2.6 Comparing Biogeographic Congruence In Morphological & Molecular Trees

Biogeographic congruence measures were compared across data type in several different ways. All statistical analyses were implemented in R (R Core Team 2017). The number of times molecular topologies were preferred over morphological ones was calculated using both paired Wilcoxon signed-rank tests on the distributions of values on morphological and molecular trees as well binomial tests. However, considering the full dataset does not take into account the fact that some topologies may have fit values which are essentially indistinguishable from a random mapping of region characters on the trees. To address this issue, the binomial test analysis was repeated on only those

datasets where at least one of the trees showed CI/RI p-values significantly different from the random distributions generated.

In order to check that these results reflected a genuine difference in the distribution of fit values and were due purely to differences in the type of data analysed, paired Wilcoxon signed-rank tests were also performed on the measures of biogeographic fit, descriptors of the source data and the probability values that CI/RI differed significantly from random. We found no support for a difference in either tree balance, as expressed by Heard's Index, or publication year between morphological and molecular datasets.

4.2.7 Testing Stratigraphic Congruence

In addition to analysing biogeographic congruence the consistency of the phylogenies with stratigraphy was assessed. Using the Paleobiology Database (Alroy 2013) and The Fossil Record 2 (Benton 1993), clades containing taxa with a good fossil record were selected from the dataset used in the biogeographic analysis. In total, sets of phylogenies for 23 clades of organisms (18 mammal, 3 reptile, 1 bird & 1 plant) were analysed. For each taxon in the clade fossil dates were used to assign first and last occurrences as stage-level time bins for all taxa with available material. Dates were only used for taxa that could be unambiguously assigned to terminal taxon groups. Taxa can only appear in the fossil record after they evolve, with low preservation potential in many cases ensuring the appearance of fossils in the record lags behind their time of origin. The 'Signor-Lipps effect' also means that taxa are likely to disappear from the fossil record prior to their real extinction as they become scarcer. In consideration of these phenomena, in cases where stratigraphy was unresolved at the stage level, taxa were assigned to the first stage in the time interval given for their first occurrence and the last stage in the time interval for their last occurrence, to represent the maximum possible range indicated by their fossil record.

4.2.8 Measures Of Stratigraphic Fit

A number of different measures of stratigraphic congruence have been proposed, therefore occurrence data were used to assess these empirically for morphological and molecular trees. Phylogenies were time-calibrated using the strap function of R and a number of measures of stratigraphic fit calculated using the GHOSTS 2.4 program (Wills 1999). A brief summary of each metric follows.

The stratigraphic consistency index, or SCI (Huelsenbeck 1994), measures the proportion of internal nodes in a tree which are stratigraphically consistent nodes, that is to say, the order of internal nodes in the tree matches the branching order inferred from the appearance of taxa in the fossil record.

$$SCI = \frac{C}{N'}$$

Where C is the number of stratigraphically consistent nodes and N' is the total number of internal nodes in the tree.

The SCI is, therefore, biased to give low values when the matching of that data is low and can give high values even in cases where consistency is due to a lack of fossil occurrences for a given group. Some authors have argued for a negative relationship between SCI and the tree size: as the number of nodes in the tree increases, as with fewer nodes it is more likely the order of branching events in the tree will perfectly match the fossil record. Simulations, however, recovered the opposite effect, with SCI increasing with the addition of taxa for random stratigraphic data (Siddall and Kluge 1997) when considering fewer than 20 taxa. This is less of a problem in this particular case where matching trees were compared for the same clade with the same fossil record, although it does limit the usefulness of the SCI more generally. However, tree shape also affects SCI, as perfectly balanced trees where each taxon appears at a different time cannot have values lower than 0.5, although there is mixed support for what effect tree shape has empirically (Siddall 1997; Hitchin and Benton 1997). There is also evidence from simulations that SCI can show high values even with random stratigraphic data (Siddall 1997) which is somewhat counterintuitive for a measure of stratigraphic fit.

The relative completeness index, or RCI (Benton and Storrs 1994), instead measures the summed gaps in the fossil record inferred from a given phylogeny. Minimum implied gaps (MIG) are calculated as the difference between the age of the first fossil occurrence of a lineage and that of its sister lineage and then summed for all internal nodes. The total MIG value is then scaled relative to the summed simple range lengths for each

taxon (i.e. the time between the first and last occurrence) and expressed as a percentage value.

$$RCI = \left(1 - \frac{\sum MIG}{\sum SRL}\right) \times 100\%$$

Negative RCI values can be generated in cases where the phylogeny implies a total gap which is greater than the ranges known from the record, while an RCI of 100% means no gaps in the fossil record are implied by the tree. Unlike the SCI, RCI will give low values when the fossil record of a group is poor, even if the order of branching events implied by the rock record and tree are identical. The RCI is, therefore, only partly affected by the fit of the tree to the record, also being affected by the completeness of the record and the occurrence ages of fossils. The most extreme illustration of this is that maximum values of 100% are impossible unless all taxa appear at the same time, as any age difference between any pair of sister lineages will contribute to the MIG. Again, tree shape biases the RCI value although the effect is less obvious than for SCI, as minimum and maximum MIG guaranteed to be possible on fully pectinate trees but not necessarily on balanced ones (Wills 1999).

Another approach, the Manhattan stratigraphic measure, or MSM (Siddall 1998), was proposed to deal with the problems in tree shape inherent to the SCI and RCI. It uses the optimization of a Sankoff character coded from the first occurrence ages of taxa. Each taxon is given a unique character state and the transformation costs of each character transition are defined by a symmetrical step matrix based on the difference in first occurrences between pairs of taxa. These transformation costs, therefore, penalise transitions between taxa with large stratigraphic gaps. The length of the character optimized onto the tree (L_o) is then compared to the minimum possible length (L_m) in a manner analogous to the CI. The original MSM was found to be insensitive to the addition of young basal taxa bracketed by older taxa (Pol and Norell 2001), which actually increased significance despite adding more conflict with stratigraphy. A modified implementation of the MSM is therefore preferred, where the character step-matrix follows Camin-Sokal parsimony rules (reversals are assigned an infinite cost to be prohibited).

$$MSM^* = \frac{L_m}{L_o}$$

A detailed investigation of biases in the MSM* is lacking but, like the previous metrics, it is in theory also affected by tree balance, with pectinate trees having higher theoretical maxima than their non-pectinate equivalents.

The last measure of stratigraphic fit we consider in this study is the gap excess ratio (Wills 1999), or GER. Unlike the other metrics that incorporate ghost ranges, this metric was formulated to account for the effect of differently distributed range data. The GER is the difference between the MIG and the minimum possible ghost range for any tree (G_{min}), given as a fraction of the range of possible values for the stratigraphic data on any tree.

$$GER = 1 - \frac{MIG - G_{min}}{G_{max} - G_{min}}$$

Where MIG is the total minimum implied gap, G_{min} is the minimum possible ghost range and G_{max} is the maximum possible ghost range. The GER in its original form is still biased to certain tree shapes, as most non-pectinate trees cannot have MIG values which reach G_{min} or G_{max} and therefore show less extreme maximum values than fully pectinate trees. The topological GER (GERt) is simply the GER calculated for a specific topology rather than any topology (Wills et al. 2008)

$$GERt = 1 - \frac{MIGu - Gt_{min}}{Gt_{max} - Gt_{min}}$$

Where MIGu is the total minimum implied gaps given in stratigraphic intervals of unit length (while ranges of millions of years could be used, this would assume uniform preservation potential), Gt_{min} and Gt_{max} are the minimum and maximum possible ghost range on a specified topology. In practice the long tails and skewed distribution of ghost ranges make it difficult to determine Gt_{min} and Gt_{max} directly, making it likely that Gt_{min} will be overestimated relative to Gt_{max} to give overestimates of GERt.

To deal with this problem, a modification of the GER (GER*) estimates the distribution of randomized MIGu values rather than the minimum and maximum ghost ranges. The GER* is the fraction of the area under a curve of randomized MIGu values which are greater than the observed MIGu.

$$GER^* = 1 - \frac{100}{\sum randomised\ strategraphic\ ghost\ ranges\ \leq\ observed\ MIGu}$$

The GER* offers a number of advantages over other measures of stratigraphic congruence. Unlike the majority of metrics, GER* estimates are relative to the expected values for a given topology, making it insensitive to differences in tree shape. The GER was originally formulated to account for differences in the distribution of ranges unlike the RCI, which is strongly affected by the distribution of ranges and the SCI, which ignores ranges entirely. Lastly, it is purely a measure of stratigraphic fit, rather than the completeness of the record (RCI), or the consistency of nodes with available data (SCI).

Binomial tests were carried out for each stratigraphic fit metric in the same way we tested biogeographic congruence, counting the number of instances the molecular tree showed better stratigraphic fit than its morphological counterpart. Additional tests were then performed to ensure that morphological and molecular trees really did show similar ranges for stratigraphic fit measures, firstly, whether morphological and molecular trees showed different distributions for measures of stratigraphic fit (SCI, MIG, RCI, MSM*,GER, GERt and GER*) using paired Wilcoxon signed-rank tests. Finally, tests of the biogeographic congruence metrics were carried out using only the clades included in the stratigraphic analyses, in order to determine how biogeographic and stratigraphic congruence differed for the same sample of clades.

4.3 Results

4.3.1 Biogeographic Fit Metrics, Dataset Size & Publication Year

Of the 48 clades analysed, 35 were within the vertebrates, 8 within plants and 5 from the invertebrates (**Table 4.1**). The majority of trees in the dataset (77 out of 96) were constructed under parsimony, with 10 Maximum parsimony and 5 Bayesian trees in the molecular partition. A small number of phylogenetic trees were constructed using other methods, with 3 morphological trees and 1 molecular tree being a consensus of previous phylogenetic studies and 1 morphological UPGMA tree. The trees varied markedly in terms of age of publication and the source data (**Table 4.2**). Number of taxa used to construct the tree ranged between 7 and 71 with the mean and median number of taxa being 25 and 20 respectively, while the number of phylogenetic characters used ranged between 1 and 43,616 with a mean of 2,682 and a median of 233. As expected, morphological datasets had markedly fewer phylogenetic characters (mean = 200, median = 91) than molecular ones (mean = 5,164, median = 2,222). The source papers for these trees were published over an interval of 36 years between 1980 and 2016, with a mean year of 2002 and a median year of 2003 for both morphological and molecular partitions. Given the range of groups studied both in terms of number of taxa and taxonomic affinity, it is unsurprising that the number of biogeographic region characters used to test phylogenetic fit also ranges between 4 and 98, with a mean of 22 and a median of 14 regions. Heard's index values showed tree shape varied between highly symmetrical trees (I*m* = 0.009) to somewhat pectinate ones (I*m* = 0.694), with the average tree being quite highly balanced (mean I*m* = 0.292, median I*m* = 0.262). Heard index values were similar for both the morphological (mean I*m* = 0.298, median I*m* = 0.265) and molecular (mean I*m* = 0.286, median = 0.256) trees.

Clade	Author	Category	Data Type
Eutheria	O'Leary et al. 2013	Morphological	Parsimony, 4541 characters,
		Molecular	Parsimony, 35,603bp, 27 nuclear genes
Canidae	Zrzavy & Ricankova 2004	Morphological	Parsimony, 188 characters, 29 craniomandibular, 36 dental, 14 postcranial, 36 soft part, 9 developmental, 48 behavioural, 14 chromasomal
		Molecular	Parsimony,235 characters CYTB, 180 characters COI,194 characters COII
Chiroptera	Simmons 2008	Morphological	Parsimony, 207 characters, 8 dentary, 15 craniomandibular, 10 inner ear, 78 postcranial, 93 soft part
	Teeling 2005	Molecular	Maximum likelihood, 17 nuclear genes 13,700bp
Megachiroptera	Giannini & Simmons 2005	Morphological	Parsimony 236 characters, Hard part (108 craniomandibular & 64 postcranial), 62 soft part (external & internal), 2 behavioural
		Molecular	Parsimony (direct optimization) 4 mitochondrial genes, 1 nuclear gene 3,500bp
Plecotini	Bogdanowicz 1998	Morphological	Parsimony 56 characters, 37 hard part (craniomandibular), 8 soft part (external), 11 karyological
	Hoofer 2001	Molecular	Parsimony 3 mitochondrial genes 2,700bp
Phyllostomid bats	Davalos et al. 2012	Morphological	Parsimony, 220 characters, hard part (craniomadibular & postcranial), soft part (external & internal), karyological
		Molecular	Maximum likelihood,5,705bp, CytB 1,140bp, 12S, tRNA-Val & 16S 2608bp, COX1 657bp, RAG2 nuclear fragment 1,300bp
Mormoopidae	Simmons 2001	Morphological	Parsimony, 209 characters, hard parts (47 craniodental & 60 postcranial), 102 soft parts (external & internal organs)
	Lewis Oritt et al. 2001	Molecular	Maximum likelihood, 2,538bp, 1 mitochondrial gene 1,140bp, 1 nuclear gene 1,398bp
Ophraella	Futuyma 1990	Morphological	Parsimony, 88 characters, 50 imago, 3 egg, 27 larva, 6 pupa
	Funk 1995	Molecular	Parsimony, 866bp, 1 rRNA, 1 mitochondrial gene
Ratites	Worthy 2012	Morphological	Parsimony 179 characters, 63 craniomandibular, 116 post cranial
	Mitchell et al. 2014	Molecular	Parsimony, mitochondrial genome 15,731bp
Epicrates	Kluge 1989	Morphological	Parsimony, 53 characters, 8 external soft parts, 39 craniomandibular, 6 postcranial
	Tolson 1987	Molecular	Parsimony, Skin & scent gland lipids, 24 characters
Heliconius	Brown 1981	Morphological	Biosystematic consensus, egg, larva, pupa, imago, behavioural, biogeographical, karyological
	Brower 1994	Molecular	Parsimony, mtDNA fragment 950bp, 3 genes
Rhopalocera	Wahlberg 2005	Morphological	Parsimony, 99 characters, 39 wing venation, 19 leg, 14 head, 21 thoracic, 2 abdominal
		Molecular	Bayesian,3159bp, COI 1531bp, EF-1a 1225bp, wingless 403bp

Table 4.1 Source papers, Data Category (Morphological/Molecular) and Data Summary for the 48 clades used in this study.

Clade	Author	Category	Data Type
Pinales	Hart 1987	Morphological	Parsimony 123 characters, 3 growth, 23 stem and wood anatomy, 16 leaf, 5 chemistry, 1 sex distribution, 7 microsporangiate strobilus, 15 microgametophyte, 27 embryo, 16 ovulate strobilus, 9 ovule and seeds, 1 cytology
	Tsumura et al. 1995	Molecular	Parsimony, 6 chloroplast genes 8091bp, frxC 779bp, rbcL 1387bp, psbA 939bp, psbD 1042bp, trnK 2569bp, 16S 1375bp
Crocodylia	Gatesy et al. 2004	Morphological	Parsimony, 163 characters, 34 postcranial, 6 osteoderm, 124 craniomandibular
	Oaks et al. 2011	Molecular	Bayesian, DNA 7,282bp, 4 mtDNA, 9 nuclear
Cupressaceae	Gadek et al. 2000	Morphological	Parsimony, 45 characters, 3 growth, 8 stem and wood, 16 leaves, 2 pollen, 5 megagametophyte and archegonia, 9 embryonic & ovular, 1 female cone, 1 chromosomal
		Molecular	Parsimony, DNA 2930bp, matK 1530bp, rbcL 1400bp
Anas	Omland 1994	Morphological	Parsimony 34 characters, adult plumage, natal plumage, soft part, trachea, skeleton
	Livezy 1991	Molecular	Parsimony, mtDNA 119 characters
Krigia	Kim & Jansen 1994	Morphological	Parsimony, 35 characters, growth, leaves, pollen, chromosomal
		Molecular	Parsimony, 514bp, rDNA ITS region 262bp, cpDNA 252bp
Physalaemus species group	Cannatella et al. 1998	Morphological	Parsimony, 12 characters, 5 craniomandibular, 2 postcranial, 5 soft part
		Molecular	Maximum likelihood, 1,757bp, 12S 1214bp, COI 543bp
Drosophila	Piano 1996	Morphological	Parsimony, 9 characters chorion ultrastructure
		Molecular	Parsimony, Yp1 gene 1,100bp
Platynini	Leibherr & Zimmerman 1998	Morphological	Parsimony, 206 characters, 44 female reproductive tract, 23 male genitalia, 139 external
	Cryan et al. 2001	Molecular	Parsimony, mtDNA & nuclear 2516bp, cytochrome oxidase II 624bp, cytochrome b 783bp, 28S rDNA 668bp, wingless 441bp
Iguanidae 1	Schulte et al. 2003	Morphological	Parsimony, 67 characters, 28 craniomandibular, 12 postcranial, 26 soft part
		Molecular	Parsimony, mtDNA 1200bp, ND1&2 876bp, tRNA 324bp
Iguanidae 2	Sites et al. 1996	Morphological	Parsimony, 90 characters, 47 craniomandibular, 22 postcranial, 21 soft part
		Molecular	Parsimony, mtDNA 959bp, ND4 gene 742bp, tRNAs 217bp
Opluridae	Titus & Frost 1996	Morphological	Parsimony, 34 characters, 10 craniomandibular, 7 postcranial, 17 soft part
		Molecular	Parsimony, mtDNA 1129bp, 12S rDNA, valine tDNA, 16S rDNA

Table 4.1 Source papers and data summary continued (1)

Clade	Author	Category	Data Type
Phyrynosomatidae	Reeder and Wiens 1996	Morphological	Parsimony, 155 characters, 60 scalation, 55 osteology, 15 colouration, 9 behaviour, 9 myology, 4 karyology, 2 protein electrophoresis, 1 life history
		Molecular	Parsimony, mtDNA 779bp, 12S rRNA gene 253bp, 16S rRNA gene 429bp
Sphenostylis	Potter & Doyle 1994	Morphological	Parsimony, 16 characters, 1 leaf, 4 inflorescence, 4 petals, 5 stamen & anther, 2 seed
		Molecular	Parsimony, cpDNA 53 mutation characters
Anolis	Jackman 1999	Morphological	Parsimony, 16 characters, 8 craniomandibular, 8 postcranial
		Molecular	Parsimony, mtDNA 1,455bp, ND2 gene, tRNA
Squamata	Estes 1988	Morphological	Parsimony, 148 characters, 88 craniomandibular, 42 postcranial, 17 soft part, 1 developmental
	Wiens 2012	Molecular	Maximum likelihood, DNA 33,717bp, 44 nuclear genes
Sciuridae	Cardini 2003	Morphological	UPGMA dendrogram, 9 landmarks
	Steppan et al. 1999	Molecular	Maximum likelihood, cytB gene 507bp
Didelphidae	Jansa et al. 2005	Morphological	Parsimony, 1 character dorsal pelage pattern
		Molecular	Maximum likelihood, DNA 4982bp, mtDNA, cytB gene 1149bp, 4 nuclear gene, BRCA1 946bp, IRBP 1158bp, SLC38 884bp, OGT 653bp
Neckeraceae	Sotiaux et al. 2009	Morphological	Parsimony, 14 characters, leaves
		Molecular	Bayesian, nuclear rDNA 242bp, 5.8S gene, rpl16 group II intron, rps4-trnT-trnL-trnF
Josiini	Miller 1996	Morphological	Parsimony, 86 characters, 59 adult, 27 larval & pupal
	Miller 1997	Molecular	Parsimony, DNA 774bp, rDNA (313bp 28S, 202bp 18S), mtDNA (461bp COII)
Ceboidea	Kay 1990	Morphological	Biosystematic consensus, dental characters
	Schneider 1993	Molecular	Parsimony, DNA 1,800bp e-globin gene
Sphenisciformes	Bertelli 2005	Morphological	Parsimony, 159 characters, 66 integument, 70 osteology, 15 myology, 7 breeding behaviour, 1 digestive tract
		Molecular	Parsimony, mtDNA 2,100bp, 12S rDNA 958bp, cytB 1142bp
Bothropis	Fenwick et al. 2008	Morphological	Parsimony, 92 characters, 38 scale, 18 external soft parts, 6 male genitalia, 2 vertebral, 28 craniomandibular
		Molecular	Maximum likelihood, 2343bp DNA, 12S rRNA, 16S rRNA, ND4, cyt b
Andira	Pennington 1996	Morphological	Parsimony, 10 characters, 1 growth habit, 1 seedling, 2 vegetative, 4 floral, 2 fruit
		Molecular	Parsimony, 38 restriction site characters (cpDNA)
Pinacea	Klymiuk 2012	Morphological	Parsimony, 54 characters, 23 bract, 17 ovuliferous scale, 8 seed structure, 6 seed position and arrangement
	Wang 2000	Molecular	Parsimony, 686bp, Chloroplast gene (545bp matK), mitochondrial gene (141bp nad5)
Diprotodontia	Horovitz et al. 2003	Morphological	Parsimony, 230 characters, 149 postcranial, 26 dental, 50 cranial, 5 soft part
	Meredith 2009	Molecular	Maximum likelihood, DNA 5894bp, ApoB, BRCA1, IRBP, Rag1, vWF

Table 4.1 Source papers and data summary continued (2)

Clade	Author	Category	Data Type
Arctoidea	Finarelli 2008	Morphological	Parsimony, 80 characters, 35 cranial, 45 dental
	Flynn et al. 2005	Molecular	Parsimony, DNA 6243bp, mitochondrial 3266bp (CYTB 1149bp, 12S 1067, ND2 1050), nuclear 2977 (TR-i-1 1491bp, IRBP 1043bp, TBG 443bp)
Chiroptera 2	Fracasso et al. 2011	Morphological	Parsimony, 239 characters, 48 dental, 93 soft part, 80 postcranial, 18 craniomandibular
	Agnarsson et al. 2011	Molecular	Bayesian, 1140bp CYTB
Talpidae	Sanchez-Villagra 2006	Morphological	Parsimony, 157 characters, 47 dental, 25 cranial, 80 postcranial, 3 soft part
	Shinohara et al. 2004	Molecular	Parsimony, 2979bp, 1,140bp CYTB, 829bp 12S rRNA, 1,010bp RAG-1
Macropodidae	Prideaux & Warburton 2010	Morphological	Parsimony, 83 characters, 48 craniodental, 35 postcranial
	Mitchell et al. 2014	Molecular	Maximum likelihood, DNA 43,616bp ,101 mitochondrial genes, 26 nuclear genes
Didelphinae	Oliveira et al. 2011	Morphological	Parsimony, 129 characters, 39 soft part, 49 craniomandibular, 45 dentary, 4 karyological
	Voss & Jansa 2009	Molecular	Maximum Likelihood, 5 nuclear genes 5977bp, 2,100bp BRCA1, 1,000bp vWF, 1158bp IRBP, 1176 DMP1, 543bp RAG1
Echymyidae	Olivares and V. 2015	Morphological	Parsimony, 62 characters, 15 dentary, 47 craniomandibular
		Molecular	Parsimony,5086bp DNA, 2 mitochondrial genes (1140bp CYTB, 932bp 12S rRNA), 3 nuclear exons (801bp growth hormone receptor exon 10, 1149bp vWF, 1064bp RAG1)
Erinaceidae	He et al. 2012	Morphological	Parsimony, 135 characters, 61 cranial, 59 dentary, 6 postcranial, 9 pelage
		Molecular	Bayesian, mtDNA 3,218bp, 982bp 12S rRNA, 1,140bp CYTB, 1,047bp ND2
Phyllostomidae 2	Carstens et al. 2002	Morphological	Parsimony, 119 characters,16 craniomandibular, 43 dentary, 54 internal soft parts, 3 postcranial, 3 skin
		Molecular	Maximum likelihood DNA 1362bp (RAG-2 gene)
Feliformia	Gaubert et al. 2005	Morphological	Parsimony, 349 characters, 99 craniomandibular, 62 external soft parts, 57 internal soft parts, 74 dentary, 57 postcranial
		Molecular	Biosystematic concensus, DNA 4026bp, 2 nuclear genes (897bp transthyretin intron I, 945bp IRBP) 2 mitochondrial genes (1,140bp CYTB, 1,044bp ND2)
Glires	Asher et al. 2005	Morphological	Parsimony, 196 characters, 79 dentary, 73 craniomandibular, 19 inner ear, 54 postcranial, 4 soft part
		Molecular	Parsimony,5623bp, mtDNA (1146bp CYTB), nuclear genes (1131bp A2AB, 1227bp IRBP, 1233bp vWF, 886bp GHR)
Chyrsochloridae	Asher et al. 2010	Morphological	Parsimony, 144 characters, 45 postcranial, 37 dentition & mandible, 62 cranium
		Molecular	Parsimony, 913bp nuclear GHR gene

Table 4.1 Source papers and data summary continued (3)

Clade	Category	Phylogenetic Characters	Publication Year	Number of taxa	Number of characters	Heard's Index (Im)
Plectonini	Morph	56	1998	10	12	0.361111
Megachiroptera	Morph	236	2005	44	17	0.095238
Mormoopidae	Morph	209	2001	15	26	0.384615
Canidae	Morph	188	2004	23	39	0.484848
Eutheria	Morph	4541	2013	19	13	0.202614
Chiroptera 1	Morph	207	2008	19	12	0.379085
Physalaemus	Morph	12	1998	10	17	0.25
Ophraella	Morph	88	1990	11	4	0.466667
Ratites	Morph	179	2012	13	7	0.393939
Epicrates	Morph	53	1987	10	6	0.694444
Phyllostomid Bats 1	Morph	220	2012	71	39	0.00993789
Heliconius	Morph	0	1994	41	22	0.311538
Rhopalocera	Morph	99	2005	57	56	0.264935
Pinales	Morph	123	1987	63	39	0.085669
Crocodylia	Morph	163	2004	23	28	0.25974
Cupressaceae	Morph	45	2000	39	20	0.146515
Krigia	Morph	35	1994	7	10	0.4
Iguanidae 1	Morph	67	2003	33	20	0.114919
Platynini	Morph	206	1998	23	6	0.268398
Drosophila	Morph	9	1996	9	4	0.107143
Anas	Morph	34	1994	9	27	0.357143
Opluridae	Morph	34	1996	10	4	0.444444
Phrynosomatidae	Morph	155	1996	40	44	0.240216
Sphenostylis	Morph	16	1994	12	7	0.309091
Anolis	Morph	16	1999	53	24	0.055807
Sciuridae	Morph	9	2003	14	9	0.384615
Didelphidae	Morph	1	2005	43	18	0.211382
Neckeraceae	Morph	14	2009	20	14	0.116959
Ceboidea	Morph	0	1993	16	12	0.542857
Sphenisciformes	Morph	159	2005	17	11	0.191667
Squamata	Morph	148	1988	19	10	0.20915
Bothropis	Morph	92	2008	41	15	0.264103

Table 4.2 Summary metrics for the 96 phylogenetic trees included in the analysis. Category (Morphological or Molecular), Number of Phylogenetic Characters used to construct the tree, Year the source tree was published, Number of Taxa analysed, Number of Characters in the Biogeographic Matrix and Heard's Index of tree imbalance (higher values indicate less symmetrical, more pectinate trees).

Clade	Category	Phylogenetic Characters	Publication Year	Number of taxa	Number of characters	Heard's Index (Im)
Andira	Morph	10	1996	20	6	0.087719
Pinacea	Morph	54	2012	45	17	0.109937
Iguanidae 2	Morph	90	1996	13	7	0.242424
Josiini	Morph	86	1997	22	12	0.452381
Diprotodontia	Morph	230	2003	21	6	0.563158
Arctoidea	Morph	80	2008	17	79	0.308333
Chiroptera 2	Morph	239	2011	22	98	0.618182
Talpidae	Morph	157	2006	12	7	0.672727
Macropodidae	Morph	83	2010	16	7	0.542857
Didelphinae	Morph	129	2011	45	25	0.194503
Eutheria	Mol	35,603	2013	19	13	0.20915
Chiroptera 1	Mol	13,700	2005	19	12	0.196078
Physalaemus	Mol	1,757	1998	10	17	0.194444
Ophraella	Mol	866	1995	11	4	0.444444
Ratites	Mol	15,731	2014	13	7	0.348485
Epicrates	Mol	24	1989	10	6	0.694444
Phyllostomid Bats 1	Mol	5,705	2012	71	39	0.189234
Heliconius	Mol	950	1981	41	22	0.144872
Rhopalocera	Mol	3,159	2005	57	56	0.201948
Pinales	Mol	8091	1995	63	39	0.177155
Crocodylia	Mol	7,282	2011	23	28	0.207792
Cupressaceae	Mol	2930	2000	39	20	0.337127
Krigia	Mol	514	1994	7	10	0.333333
Iguanidae 1	Mol	1200	2003	33	20	0.302419
Platynini	Mol	2,516	2001	23	6	0.316017
Drosophila	Mol	1100	1996	9	4	0.214286
Anas	Mol	119	1991	9	27	0.321429
Opluridae	Mol	1129	1996	10	4	0.444444
Phrynosomatidae	Mol	779	1996	40	44	0.202429
Sphenostylis	Mol	53	1994	12	7	0.436364
Anolis	Mol	1,455	1999	53	24	0.239065
Sciuridae	Mol	507	2003	14	9	0.115385
Didelphidae	Mol	4982	2005	43	18	0.101045
Neckeraceae	Mol	242	2009	20	14	0.385965
Ceboidea	Mol	1,800	1993	16	12	0.114286
Sphenisciformes	Mol	2,100	2005	17	11	0.183333
Squamata	Mol	33,717	2012	19	10	0.27451
Bothropis	Mol	2343	2008	41	15	0.352564
Andira	Mol	38	1996	20	6	0.222222
Pinacea	Mol	686	2000	45	17	0.108879
Iguanidae 2	Mol	959	1996	13	7	0.469697
Josiini	Mol	774	1997	22	12	0.133333

Table 4.2 Summary metrics for the 96 phylogenetic trees continued (1)

Clade	Category	Phylogenetic Characters	Publication Year	Number of taxa	Number of characters	Heard's Index (Im)
Diprotodontia	Mol	5,894	2009	21	6	0.436842
Arctoidea	Mol	6243	2008	17	79	0.375
Chiroptera 2	Mol	1140	2011	22	98	0.328571
Talpidae	Mol	2,979	2006	12	7	0.618182
Macropodidae	Mol	43,616	2010	16	7	0.390476
Didelphinae	Mol	5,977	2011	45	25	0.172304
Echymyidae	Mol	5,086	2015	16	14	0.390476
Erinaceidae	Mol	3,218	2012	22	24	0.147619
Phyllostomidae 2	Mol	1,362	2002	21	28	0.252632
Feliformia	Mol	4,026	2005	53	85	0.11463
Glires	Mol	5,623	2005	22	56	0.257143
Chyrsochloridae	Mol	913	2010	18	9	0.110294

Table 4.2 Summary metrics for the 96 phylogenetic trees continued (2)

Region characters showed a range of fit values for the metrics used (**Table 4.3**). CI values ranged between 0.089 and 0.708 but were generally low (mean = 0.312, median = 0.277). RI showed both slightly greater ranges (0 to 0.861) and lower averages than CI (mean = 0.249, median = 0.2). Probability values from the randomisation tests ranged from less than 0.001 to 0.872 but with low averages (mean = 0.137, median = 0.023) indicating many of the observed CI and RI values are significantly better than expected. HER values were slightly lower still, ranging from -0.228 to 0.775 with a mean of 0.158 and a median of 0.133. Shapiro-Wilks tests performed on both the metrics of fit and dataset summary metrics showed that the majority of data partitions were non-normally distributed (**Table 4.4**). Only a few of the metrics were normally distributed, namely the morphological (W = 0.962, p = 0.122) and molecular (W = 0.965, p = 0.160) tree publication dates when considered separately (but not together), Heard's index values for the morphological trees (W = 0.957, p = 0.076) and CI values from morphological trees (W = 0.960, p = 0.102). Due to most of the tests confirming non-normal distributions, non-parametric tests were used for statistical analysis.

Clade	Category	CI	RI	p-Value	HER
Plectonini	Morph	0.5	0.333333	0.019498	0.23859801
Megachiroptera	Morph	0.207317	0.22619	0.0007	0.15873614
Mormoopidae	Morph	0.273684	0.316832	0.09989	0.12910787
Canidae	Morph	0.33913	0.146067	0.024698	0.10101089
Eutheria	Morph	0.1912	0.2667	0.284272	0.05252622
Chiroptera 1	Morph	0.3158	0.6667	0.0001	0.46232598
Physalaemus	Morph	0.68	0.2	0.077592	0.10472482
Ophraella	Morph	0.363636	0	0.79752	-0.2281779
Ratites	Morph	0.538462	0.538462	0.0009	0.48014591
Epicrates	Morph	0.6	0	0.252175	-0.0977671
Phyllostomid Bats 1	Morph	0.091335	0.333333	0.0006	0.14220533
Heliconius	Morph	0.1128	0.2575	0.120788	0.05555107
Rhopalocera	Morph	0.089314	0.124233	0.210179	0.02828491
Pinales	Morph	0.161157	0.8607	0.0003	0.14857743
Crocodylia	Morph	0.405797	0.254545	0.0007	0.23064943
Cupressaceae	Morph	0.294118	0.076923	0.065893	0.04394849
Krigia	Morph	0.434783	0.133333	0.334667	-0.0061686
Iguanidae 1	Morph	0.30303	0.432099	0.0001	0.35777601
Platynini	Morph	0.222222	0.086957	0.348765	-0.0046309
Drosophila	Morph	0.444444	0	0.310169	-0.076519
Anas	Morph	0.40625	0.309091	0.09609	0.12881503
Opluridae	Morph	0.571429	0.625	0.0035	0.52680642
Phrynosomatidae	Morph	0.184874	0.208163	0.013099	0.09724488
Sphenostylis	Morph	0.368421	0.076923	0.337066	-0.0145075
Anolis	Morph	0.23913	0.102564	0.008899	0.06964875
Sciuridae	Morph	0.428571	0.4	0.0006	0.32919671
Didelphidae	Morph	0.104651	0.129944	0.339366	0.0106166
Neckeraceae	Morph	0.4375	0.217391	0.516548	-0.0353971
Ceboidea	Morph	0.27907	0.261905	0.166983	0.0859906
Sphenisciformes	Morph	0.268293	0.166667	0.267073	0.03598352
Squamata	Morph	0.153846	0.179104	0.741326	-0.0753655
Bothropis	Morph	0.174419	0.236559	0.010999	0.11361684
Andira	Morph	0.375	0.090909	0.026497	0.08122014
Pinacea	Morph	0.234043	0.370968	1E-04	0.33296894
Iguanidae 2	Morph	0.4375	0.25	0.039096	0.15275777
Josiini	Morph	0.226415	0.145833	0.450555	-0.0076161
Diprotodontia	Morph	0.428571	0.578947	1E-04	0.49023806
Arctoidea	Morph	0.232653	0.173815	0.80482	-0.072929

Table 4.3 Summary of fit metrics for the 96 phylogenetic trees included in the analysis. Category (Morphological or Molecular), Consistency Index (CI), Retention Index (RI), probability of CI & RI values falling within the null distribution (p-Value) and Homoplasy Excess Ratio (HER).

Clade	Category	CI	RI	p-Value	HER
Chiroptera 2	Morph	0.189043	0.176704	0.0002	0.33230828
Talpidae	Morph	0.401045	0.120195	0.024698	0.24225203
Macropodidae	Morph	0.212302	0.206428	0.021998	0.19808151
Didelphinae	Morph	0.12561	0.136958	0.012899	0.11091583
Echymyidae	Morph	0.268208	0.164104	0.568143	-0.0402742
Erinaceidae	Morph	0.391801	0.019175	0.0003	0.14142363
Phyllostomid Bats 2	Morph	0.202952	0.187454	0.025297	0.15841902
Feliformia	Morph	0.109836	0.092048	0.0033	0.13918495
Glires	Morph	0.237389	0.119981	0.014199	0.15190304
Chyrsochloridae	Morph	0.298688	0.078498	0.275472	0.00919093
Plectonini	Mol	0.521739	0.388889	0.010799	0.28356031
Megachiroptera	Mol	0.223684	0.297619	1E-04	0.22455964
Mormoopidae	Mol	0.270833	0.306931	0.124388	0.11753657
Canidae	Mol	0.325	0.089888	0.090691	0.06543848
Eutheria	Mol	0.26	0.5067	0.002	0.36167166
Chiroptera 1	Mol	0.2791	0.6026	0.0001	0.46284477
Physalaemus	Mol	0.708333	0.3	0.041296	0.17009497
Ophraella	Mol	0.363636	0	0.80062	-0.2230279
Ratites	Mol	0.538462	0.538462	0.001999	0.47920735
Epicrates	Mol	1	1	1E-04	0.77472911
Phyllostomid Bats 1	Mol	0.098985	0.390034	1E-04	0.22209001
Heliconius	Mol	0.108374	0.223176	0.205379	0.03648322
Rhopalocera	Mol	0.08903	0.121166	0.486551	-0.0022117
Pinales	Mol	0.152941	0.149606	0.005999	0.09134048
Crocodylia	Mol	0.41791	0.290909	0.001	0.23431224
Cupressaceae	Mol	0.30303	0.115385	0.026397	0.07553112
Krigia	Mol	0.47619	0.266667	0.224778	0.08991627
Iguanidae 1	Mol	0.31746	0.469136	1E-04	0.39045913
Platynini	Mol	0.25	0.217391	0.010399	0.15442541
Drosophila	Mol	0.5	0.2	0.106789	0.0990991
Anas	Mol	0.440678	0.4	0.014499	0.24851405
Opluridae	Mol	0.571429	0.625	0.005599	0.51799486
Phrynosomatidae	Mol	0.176707	0.163265	0.114389	0.04677011
Sphenostylis	Mol	0.368421	0.076923	0.476052	-0.0488044
Anolis	Mol	0.323529	0.410256	1E-04	0.36348654
Sciuridae	Mol	0.391304	0.3	0.0023	0.24116362
Didelphidae	Mol	0.113924	0.20904	0.053395	0.10720812
Neckeraceae	Mol	0.378378	0	0.013199	0.14045861

Table 4.3 Summary of fit metrics for the 96 phylogenetic trees included in the analysis continued (1)

Clade	Category	CI	RI	p-Value	HER
Ceboidea	Mol	0.25	0.142857	0.558044	-0.0374401
Sphenisciformes	Mol	0.275	0.194444	0.140286	0.08450638
Squamata	Mol	0.16129	0.223881	0.49705	-0.0150679
Bothropis	Mol	0.178571	0.258065	0.0038	0.14092556
Andira	Mol	0.4	0.181818	0.031697	0.13644214
Pinacea	Mol	0.22	0.419355	1E-04	0.2790861
Iguanidae 2	Mol	0.466667	0.333333	0.016498	0.23018447
Josiini	Mol	0.214286	0.083333	0.872213	-0.0398582
Diprotodontia	Mol	0.545455	0.736842	0.0005	0.67972738
Arctoidea	Mol	0.230181	0.162517	0.128687	0.08844907
Chiroptera 2	Mol	0.189042	0.176875	0.0043	0.204287
Talpidae	Mol	0.403791	0.129329	0.0002	0.52143951
Macropodidae	Mol	0.213773	0.212985	0.028797	0.19139957
Didelphinae	Mol	0.126972	0.14747	0.012199	0.11156585
Echymyidae	Mol	0.268953	0.167063	0.19978	0.06042756
Erinaceidae	Mol	0.402674	0.061739	0.0024	0.15856552
Phyllostomid Bats 2	Mol	0.201217	0.178712	0.012799	0.18528281
Feliformia	Mol	0.111745	0.109266	0.0004	0.19197351
Glires	Mol	0.23737	0.119659	0.017698	0.15221366
Chyrsochloridae	Mol	0.302866	0.096061	0.072993	0.08613425

Table 4.3 Summary of fit metrics for the 96 phylogenetic trees included in the analysis continued (2)

Metric	Data Partition	Shapiro-Wilk W value	p-Value	Normally Distributed
Phylogenetic Characters	All	0.953	0.002	No
	Morphological	0.223	3.222×10^{-14}	No
	Molecular	0.536	4.33×10^{-11}	No
NTax	All	0.849	2.331×10^{-8}	No
NChar	All	0.752	2.689×10^{-11}	No
Publication Year	All	0.968	0.018	No
	Morphological	0.962	0.122	Yes
	Molecular	0.965	0.160	Yes
I*m*	All	0.932	0.008	No
	Morphological	0.957	0.076	Yes
	Molecular	0.939	0.014	No
CI	All	0.927	5.697×10^{-5}	No
	Morphological	0.960	0.102	Yes
	Molecular	0.898	0.001	No
RI	All	0.872	1.649×10^{-7}	No
	Morphological	0.868	6.851×10^{-5}	No
	Molecular	0.875	0.001	No
p-Value	All	0.676	4.265×10^{-13}	No
	Morphological	0.743	8.167×10^{-8}	No
	Molecular	0.600	3.278×10^{-10}	No
Biogeographic HER	All	0.945	0.001	No
	Morphological	0.743	8.167×10^{-8}	No
	Molecular	0.600	3.278×10^{-10}	No

Table 4.4 Results of Shapiro-Wilks tests for normality on metrics of interest: number of phylogenetic characters (Phylogenetic Characters), number of taxa (NTax), number of region characters (NChar),), year in which the source paper for the tree was published (Publication Year), Heard's Index of tree balance (I*m*), Consistency Index (CI), Retention Index (RI), probability of CI & RI values falling within the null distribution (p-Value) and the biogeographic Homoplasy Excess Ratio (Biogeographic HER).

4.3.2 Correlation Of Fit Metrics With Number Of Phylogenetic Characters, Number Of Region Characters & Publication Year

To test whether variables other than data type (whether a tree was constructed using morphology or molecules) had an effect on CI, RI and biogeographic HER values, a number of nested linear models were fitted with each fit metric as the dependent variable (**Table 4.5**). Model fit was then evaluated using the Akaike weight criterion (AIC). AIC values revealed that CI was not predicted particularly well by data type (AIC = -76.68, t =-0.522, p = 0.603), being most strongly negatively correlated with number of taxa (AIC = -130.7, R^2 = 0.4262, p = < 0.001), followed by number of region characters (AIC = -97.458, R^2 = 0.188, p = <0.001). CI also negatively correlated with publication year (AIC = -82.757, R^2 = 0.054, p = 0.013), possibly due to the strong tendency for more recent studies to include greater numbers of taxa (greater numbers of taxa also allow more regions to be coded with unique taxon compositions). The best supported model contained publication year, number of taxa and number of region characters (AIC = -136.3), although a model containing only numbers of taxa and region characters received only slightly less support (AIC = -135.1). RI values showed strongest correlation with the number of region characters (AIC = -45.6, R^2 = 0.020, p = 0.092) followed by the number of phylogenetic characters used to make the trees (AIC = -44.18, R^2 = 0.005, p = 0.228), then data type (AIC = -43.559, t = -0.927, p = 0.356). Support was strongest for the model including only number of region characters (AIC = -45.6), with slightly lower support for a model including number of region and phylogenetic characters (AIC = -45.59). Lastly, biogeographic HER values were most strongly correlated with publication year (AIC = -57.617, R^2 = 0.034, p = 0.040), followed by the data type (AIC = -56.565, t = -1.805, p = 0.074). Biogeographic HER values also showed a weaker correlation with the number of phylogenetic characters in the dataset (AIC = -54.77, R^2 = 0.023, p = 0.074). The best supported model included publication year, data type and number of phylogenetic characters used to build the trees (AIC = -60.38), although the addition of number of biogeographic characters as a variable lowered likelihood support only slightly (AIC = -60.04).

Model Number	Model	CI	RI	Biogeographic HER
1	Fit~Year	-82.76	-42.83	-57.62
2	Fit~Year+NTax	-133.4	-40.83	-56.39
3	Fit~Year+NChar	-98.57	-43.6	-57.21
4	Fit~Year+Type	-81.18	-41.73	-58.73
5	Fit~Year+Size	-81.45	-42.77	-58.61
6	Fit~Year+NTax+NChar	-136.3	-42.19	-55.39
7	Fit~Year+NTax+Type	-132.1	-39.74	-57.51
8	Fit~Year+NTax+Size	-132	-40.78	-57.27
9	Fit~Year+NChar+Type	-97.03	-42.5	-58.33
10	Fit~Year+NChar+Size	-97.39	-43.59	-58.24
11	Fit~Year+Type+Size	-79.97	-41.94	-60.38
12	Fit~Year+NTax+NChar+Type	-135	-41.11	-56.51
13	Fit~Year+NTax+NChar+Size	-134.90	-42.31	-56.36
14	Fit~Year+NTax+Type+Size	-130.70	-39.95	-59.05
15	Fit~Year+NChar+Type+Size	-95.96	-42.76	-60.04
16	Fit~Year+NTax+NChar+Type+Size	-133.7	-41.49	-58.16
17	Fit~NTax	-130.7	-42.69	-53.62
18	Fit~NTax+NChar	-135.1	-44.19	-51.94
19	Fit~NTax+Type	-130.7	-42.69	-53.62
20	Fit~NTax+Size	-129.42	-42.66	-54.15
21	Fit~NTax+NChar+Type	-133.6	-43.1	-53.23
22	Fit~NTax+NChar+Size	-133.8	-44.31	-52.5
23	Fit~NTax+Type+Size	-127.9	-43.49	-56.07
24	Fit~NTax+NChar+Type+Size	-132.4	-43.49	-54.44
25	Fit~NChar	-97.46	-45.6	-53.86
26	Fit~NChar+Type	-95.8	-44.5	-55.15
27	Fit~NChar+Size	-96.36	-45.59	-54.46
28	Fit~NChar+Type+Size	-94.81	-44.76	-56.4
29	Fit~Type	-76.68	-43.56	-56.56
30	Fit~Type+Size	-75.57	-43.8	-57.82
31	Fit~Size	-77.92	-44.18	-54.77

Table 4.5 Akaike Information Criterion (AIC) values for linear models of fit metrics (Fit) as a product of publication date (Year), number of taxa (NTax), number of biogeographic characters (NChar), and whether the dataset is morphological or molecular (Type). Metrics tested for Fit were the Consistancy Index (CI), Retention Index (RI) and biogeographic Homoplasy Excess Ratio (Biogeographic HER).

Both year of publication and the number of phylogenetic characters used to construct the trees indirectly represent an improvement in phylogenetic information and could, therefore, conceivably impact our measures of biogeographic congruence. To investigate whether this was the case each metric was plotted against the number of phylogenetic characters (**Fig. 4.2**) and publication year (**Fig. 4.3**). Breusch-Pagan tests showed residual variance was low for all combinations of metrics with the number of phylogenetic characters and most combinations with publication year (**Table 4.6**). However, as a few of the datasets showed numbers of phylogenetic characters that were substantially larger than the rest, Pearson correlation coefficients were only calculated for a subset of the data with outliers removed.

Spearman rank correlations showed the strongest correlation was a positive relationship between the number of phylogenetic characters (hereafter, Size) and the publication year (**Table 4.7**). A positive correlation was also found between Size and the number of taxa (hereafter, NTax) but only for morphological trees. Size showed a significant negative correlation with CI and a positive correlation with Biogeographic HER, but only across the total combined dataset and the sample of morphological trees. Therefore, CI is implying region characters tend to show worse fit onto trees constructed using more characters, while Biogeographic HER is implying the reverse is true. There was no evidence for a significant correlation between either RI or Heard's Index (I*m*) and Size. The p-values from the randomisation of CI and RI values did negatively correlate across the whole dataset and the morphological (but not molecular) subset, that is, the fits of region characters were more likely to differ from random on trees constructed from larger matrices. Analysis of Spearman rank correlations after outliers were removed produced results which were in most cases highly similar to the full dataset, although with greater support for a correlation with NTax and support for positive correlations between the number of region characters (hereafter, NChar) and Size. This is likely as datasets with more taxa tend to have both larger numbers of phylogenetic characters and a larger number of regions in which those taxa are present. Pearson tests for correlation supported linear correlations between the number of phylogenetic characters and these variables in a smaller number of cases, suggesting the correlations found for NTax in the morphological tree sample and NChar across the whole dataset are non-linear. Pearson tests also failed to find linear correlations between fit metrics and the number of phylogenetic characters (**Fig. 4.2**). Only the negative relationship between the CI and number of phylogenetic characters was supported in the morphological (r = -0.389, p = 0.008) and molecular (r = -0.332 p = 0.030) subsets, but not across the entire dataset.

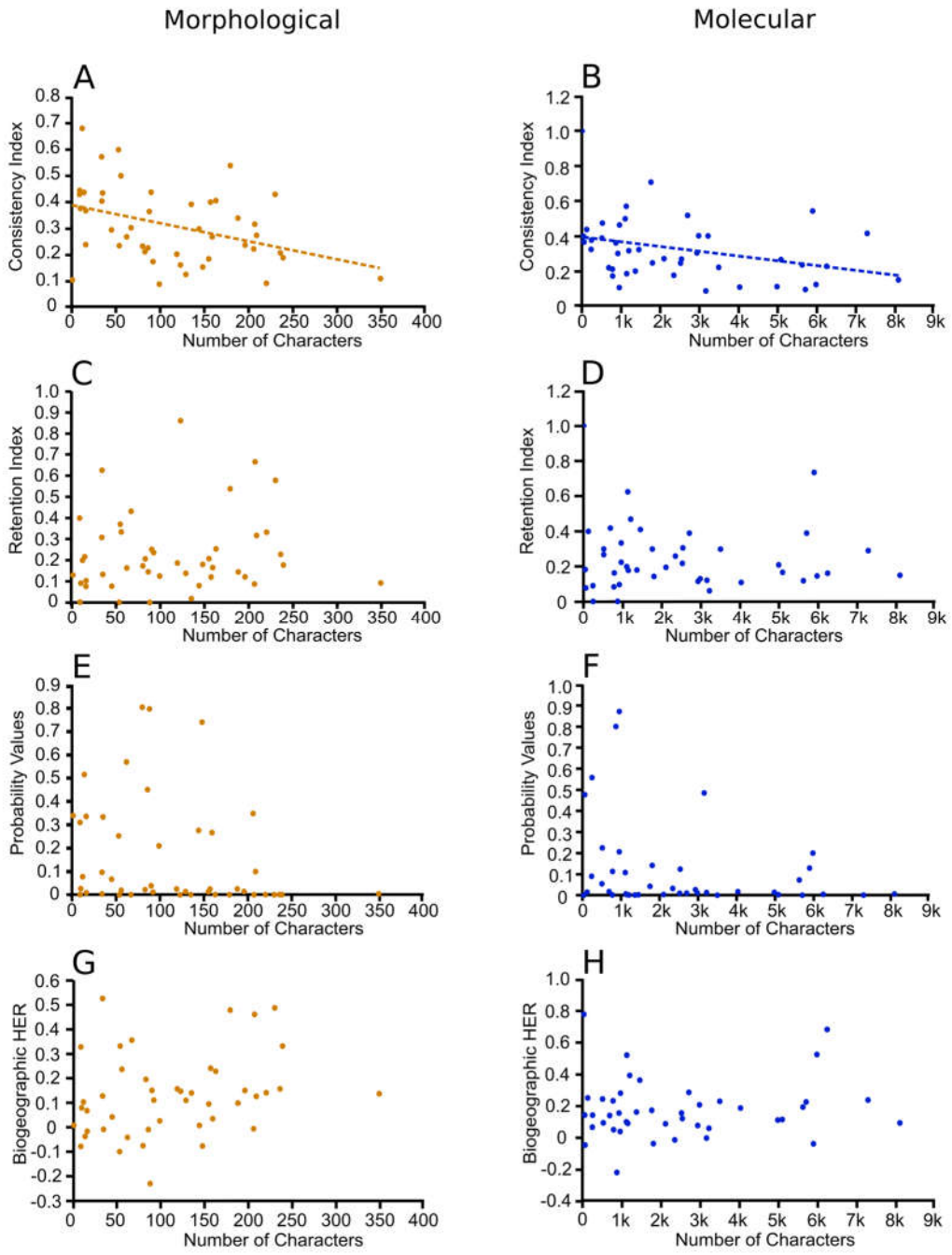

Fig. 4.2: Scatterplots of the number of phylogenetic characters (x) vs. biogeographic fit metrics (y), with outliers removed. Dotted trendlines indicate statistically significant linear regression lines. **A**: Consistency Index values for morphological trees ($R^2 = 0.151$, $p = 0.008$), **B**: Consistency Index values for molecular trees ($R^2 = 0.110$, $p = 0.030$), **C**: Retention Index values for morphological trees, **D**: Retention Index values for molecular trees, **E**: Randomization p-Values for morphological trees, **F**: Randomization p-Values for molecular trees, **G**: Biogeographic Homoplasy Excess Ratio values for morphological trees, **H**: Biogeographic Homoplasy Excess Ratio values for molecular trees.

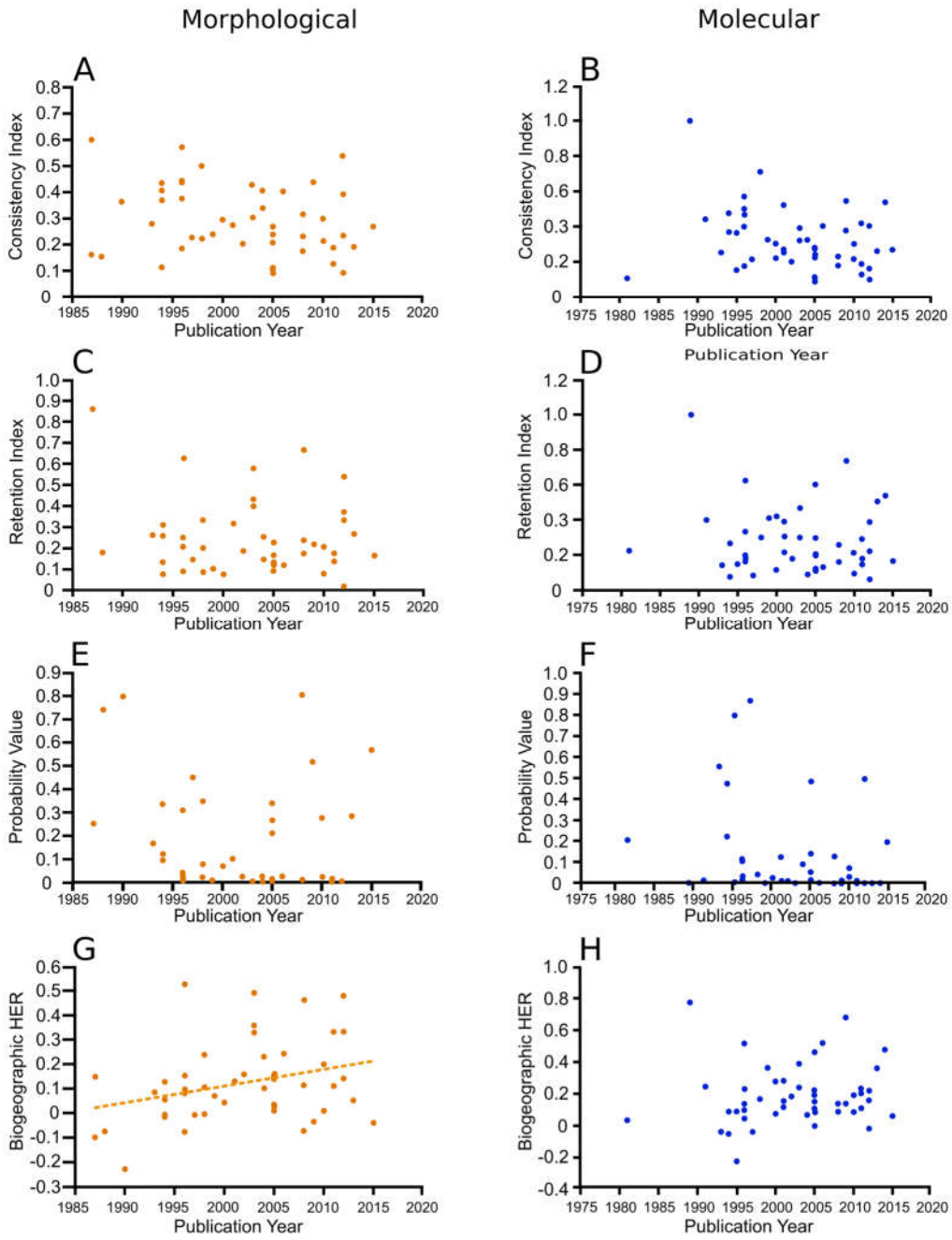

Fig. 4.3 Scatterplots of publication year (x) vs. biogeographic fit metrics (y), with outliers removed. Dotted trendlines indicate statistically significant linear regression lines. **A**: Consistency Index values for morphological trees, **B**: Consistency Index values for molecular trees, **C**: Retention Index values for morphological trees, **D**: Retention Index values for molecular trees, **E**: Randomization p-values for morphological trees, **F**: Randomization p-Values for molecular trees, **G**: Biogeographic Homoplasy Excess Ratio values for morphological trees ($R^2 = 0.1$, $p = 0.029$), **H**: Biogeographic Homoplasy Excess Ratio values for molecular trees.

Metric	Data Partition	Phylogenetic Characters		Publication Year	
		BP	p-Value	BP	p-Value
NTax	All	0.367	0.545	0.125	0.724
	Morphological	0.273	0.601	0.066	0.797
	Molecular	0.396	0.529	0.067	0.796
NChar	All	0.306	0.580	5.234	0.022
	Morphological	< 0.001	0.992	2.867	0.090
	Molecular	0.372	0.542	2.399	0.121
Phylogenetic Characters	All	NA	NA	5.510	0.019
	Morphological	NA	NA	2.427	0.119
	Molecular	NA	NA	4.672	0.031
Publication Year	All	1.220	0.269	NA	NA
	Morphological	0.805	0.370	NA	NA
	Molecular	0.552	0.457	NA	NA
I*m*	All	2.264	0.132	0.919	0.338
	Morphological	0.538	0.463	0.052	0.819
	Molecular	1.295	0.255	3.040	0.081
CI	All	0.483	0.487	6.873	0.009
	Morphological	0.707	0.401	2.074	0.150
	Molecular	0.647	0.421	5.682	0.017
RI	All	0.039	0.844	4.073	0.044
	Morphological	0.156	0.693	2.944	0.086
	Molecular	0.101	0.750	1.380	0.240
p-value	All	0.130	0.719	1.494	0.222
	Morphological	0.294	0.588	0.106	0.745
	Molecular	0.068	0.794	2.060	0.151
Biogeographic HER	All	0.023	0.878	1.196	0.274
	Morphological	0.337	0.561	0.285	0.593
	Molecular	0.036	0.850	1.937	0.164

Table 4.6 Results of Breusch-Pagan tests for heteroskedasticity on metrics of interest: number of taxa (NTax), number of region characters (NChar), number of phylogenetic characters (Phylogenetic Characters), year in which the source paper for the tree was published (Publication Year), Heard's Index of tree balance (Im), Consistency Index (CI), Retention Index (RI), probability of CI & RI values falling within the null distribution (p-value) and the biogeographic Homoplasy Excess Ratio (Biogeographic HER). Statistically significant results are highlighted in green.

Metric	Data Partition	Spearman's rho (R_S)	p-Value	Spearman's rho (R_S), no outliers	p-Value	Pearson's *r*, no outliers	p-Value
NTax	All	0.200	0.051	0.260	0.013	0.247	0.018
	Morphological	0.306	0.034	0.369	0.013	0.270	0.073
	Molecular	0.280	0.054	0.438	0.003	0.432	0.004
NChar	All	0.173	0.092	0.256	0.014	0.201	0.057
	Morphological	0.277	0.057	0.328	0.028	0.457	0.002
	Molecular	0.215	0.142	0.407	0.007	0.336	0.028
Publication Year	All	0.406	<0.001	0.338	0.001	0.302	0.004
	Morphological	0.435	0.002	0.344	0.021	0.303	0.043
	Molecular	0.663	<0.001	0.583	<0.001	0.516	<0.001
I*m*	All	-0.081	0.435	-0.096	0.365	-0.121	0.252
	Morphological	0.006	0.968	0.096	0.530	0.056	0.714
	Molecular	-0.109	0.459	-0.159	0.309	-0.178	0.254
CI	All	-0.212	0.038	-0.220	0.036	-0.183	0.083
	Morphological	-0.319	0.027	-0.384	0.009	-0.389	0.008
	Molecular	-0.329	0.022	-0.354	0.020	-0.332	0.030
RI	All	0.144	0.160	0.071	0.503	0.007	0.945
	Morphological	0.124	0.401	0.172	0.259	0.131	0.390
	Molecular	0.133	0.369	-0.025	0.871	-0.053	0.736
p-value	All	-0.232	0.023	-0.232	0.027	-0.167	0.114
	Morphological	-0.325	0.024	-0.358	0.016	-0.254	0.093
	Molecular	-0.208	0.156	-0.211	0.173	-0.220	0.156
Biogeographic HER	All	0.263	0.010	0.230	0.028	0.106	0.319
	Morphological	0.321	0.026	0.343	0.021	0.274	0.069
	Molecular	0.159	0.280	0.081	0.605	0.039	0.804

Table 4.7 Results of tests for correlation between number of phylogenetic characters and the following metrics: number of taxa (NTax), number of region characters (NChar), year in which the source paper for the tree was published (Publication Year), Heard's Index of tree balance (Im), Consistency Index (CI), Retention Index (RI), probability of CI & RI values falling within the null distribution (p-value) and the biogeographic Homoplasy Excess Ratio (Biogeographic HER). Spearman's rank-order correlations were calculated for the whole dataset, as well as for a subset of the data in which outlying high values were removed before calculating correlation coefficients. Pearson correlation coefficients were only calculated for the dataset with outliers removed. Statistically significant results are highlighted in green.

The year of publication showed a generally similar if slightly weaker set of correlations than the number of phylogenetic characters (**Table 4.8** & **Fig. 4.3**). Out of the fit metrics, CI showed a slight negative correlation but only across the dataset as a whole, while Biogeographic HER showed slight positive correlations for the whole dataset and the morphological subset of trees. As with the number of phylogenetic characters, RI and I*m* showed no evidence of correlation with publication year and the randomisation p-values showed a slight negative correlation. More recently published trees were, therefore, more likely to have better fit according to HER, worse fit according to CI and were more likely to show fit which significantly deviated from the expected null. There was also support for positive correlations for both NTax across the whole sample and morphological trees and NChar across the whole sample, indicating more recently published phylogenies tended to contain higher numbers of taxa and this resulted in a greater number of region characters, although support was weaker than that found for the number of phylogenetic characters. Pearson correlations were generally in agreement with the Spearman-rho

results, although they failed to support a relationship between publication year and Biogeographic HER across the whole dataset. The only sub-partition to show a significant trend was the morphological tree sample for Biogeographic HER (r = 0.316, p-value = 0.029).

Metric	Data Partition	Spearman's rho value (R_S)	p-Value	Pearson's r	p-Value
NTax	All	0.284	0.005	0.180	0.088
	Morphological	0.308	0.033	0.177	0.229
	Molecular	0.258	0.076	0.097	0.510
NChar	All	0.238	0.019	0.270	0.010
	Morphological	0.278	0.056	0.243	0.096
	Molecular	0.200	0.172	0.193	0.188
I*m*	All	-0.080	0.438	-0.082	0.424
	Morphological	-0.105	0.479	-0.089	0.549
	Molecular	-0.042	0.775	-0.073	0.623
CI	All	-0.239	0.019	-0.267	0.011
	Morphological	-0.245	0.093	-0.246	0.092
	Molecular	-0.228	0.120	-0.266	0.068
RI	All	0.038	0.715	-0.099	0.351
	Morphological	0.101	0.494	0.009	0.953
	Molecular	-0.032	0.828	-0.090	0.544
p-value	All	-0.284	0.005	-0.237	0.024
	Morphological	-0.281	0.053	-0.193	0.189
	Molecular	-0.274	0.060	-0.258	0.077
Biogeographic HER	All	0.257	0.012	0.181	0.087
	Morphological	0.292	0.044	0.316	0.029
	Molecular	0.184	0.210	0.112	0.449

Table 4.8 Results of tests for correlation between the publication year and the following metrics: number of taxa (NTax), number of region characters (NChar), Heard's Index of tree balance (I*m*), Consistency Index (CI), Retention Index (RI), probability of CI & RI values falling within the null distribution (p-value) and the biogeographic Homoplasy Excess Ratio (Biogeographic HER). Statistically significant results are highlighted in green.

Together these results suggest that the biogeographic congruence of phylogenies is increasing over time. If one accepts the assumption that estimates of phylogeny are also improving over time, this would suggest that the fit of regions onto trees represents an underlying phylogenetic signal, rather than being purely an artefact. The only exception to this are the CI values, which show a negative correlation with both number of phylogenetic characters and publication year. However, as both the number of phylogenetic characters and publication year correlated positively with number of taxa and region characters this negative trend is likely due to the bias CI shows towards lower values with higher numbers of taxa and characters.

4.3.3 Difference In Biogeographic Fit Between Morphological & Molecular Trees

Due to correlations between biogeographic fit metric values and other variables (see above), it was important to test for differences in these variables as well as CI, RI, randomization p-values and Biogeographic HER (**Table 4.9**). As both the number of taxa and the number of region characters were identical for each pair of trees evaluated we omitted these variables from the analysis. Paired Wilcoxon signed-rank tests indicated no significant difference between the publication years (V = 32, p = 0.362) and Heard's Index I*m* values (V = 547, p = 0.743) of morphological and molecular trees, although a significant difference was found for the number of phylogenetic characters (V = 2, p = <0.001). Contrastingly, CI (V = 305, p = 0.027), RI (V = 295, p =0.020) and Biogeographic HER (V = 288, p = 0.002) were found to significantly differ between partitions (**Fig. 4.4 & 4.5**), although no difference was found for the p-values of the CI and RI randomizations (**Fig. 4.5**: V = 662, p = 0.104). In all cases where there was a significant difference, differences between the molecular and morphological trees were skewed towards positive values, indicating fit metric values for molecular trees were higher than their morphological counterparts.

Metric	Wilcoxon Signed-Rank test statistic (V)	p-Value
Publication Year	32	0.362
Phylogenetic Characters	2	<0.001
I*m*	547	0.743
CI	305	0.027
RI	295	0.020
CI/RI Randomization p-value	662	0.104
Biogeographic HER	288	0.002

Table 4.9 Results of paired Wilcoxon signed-rank tests on the two data partitions (Morphological & Molecular) for the following metrics: publication year, number of phylogenetic characters, Heard's Index of tree balance (I*m*), Consistency Index (CI), Retention Index (RI), probability of CI & RI values falling within the null distribution (CI/RI Randomization p-value) and Homoplasy Excess Ratio (Biogeographic HER). Statistically significant results are highlighted in green.

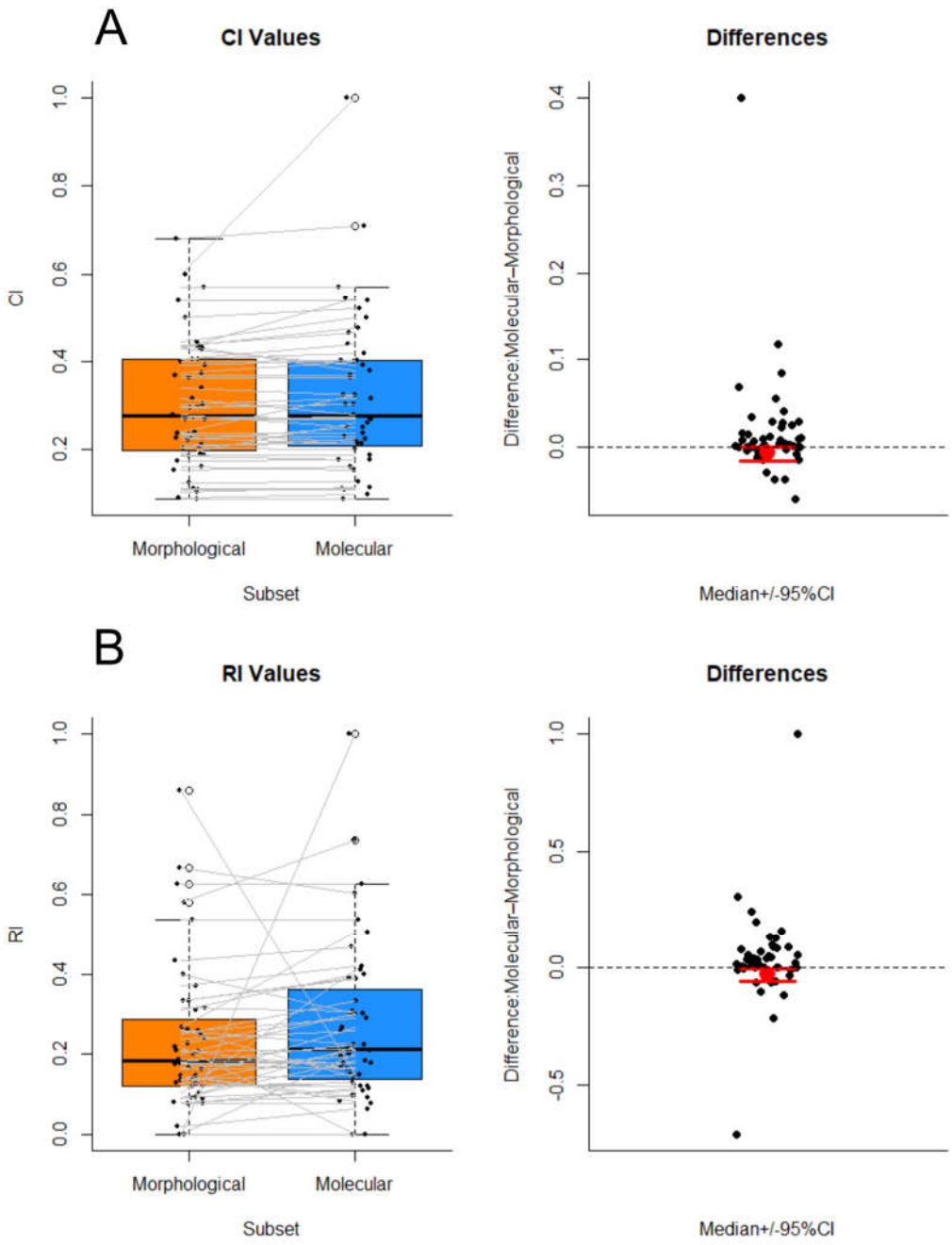

Fig. 4.4 Boxplots of raw values and differences in values between morphological and molecular trees for **A:** Consistency Index (V = 305, p =0.027) and **B:** Retention Index (V = 295, p =0.020). Boxes delimit the upper and lower quartiles of the data, while central bars are median values. Whiskers delimit plus or minus 1.5 times the inter-quartile range, from the first and third quartiles. Grey lines connect pairs of values from the same clade. Differences given are molecular values minus morphological, with positive differences indicating higher values in the molecular subsample. In the null case, difference values would be randomly distributed around the estimated pseudomedian shown in red, with upper and lower 95% confidence intervals.

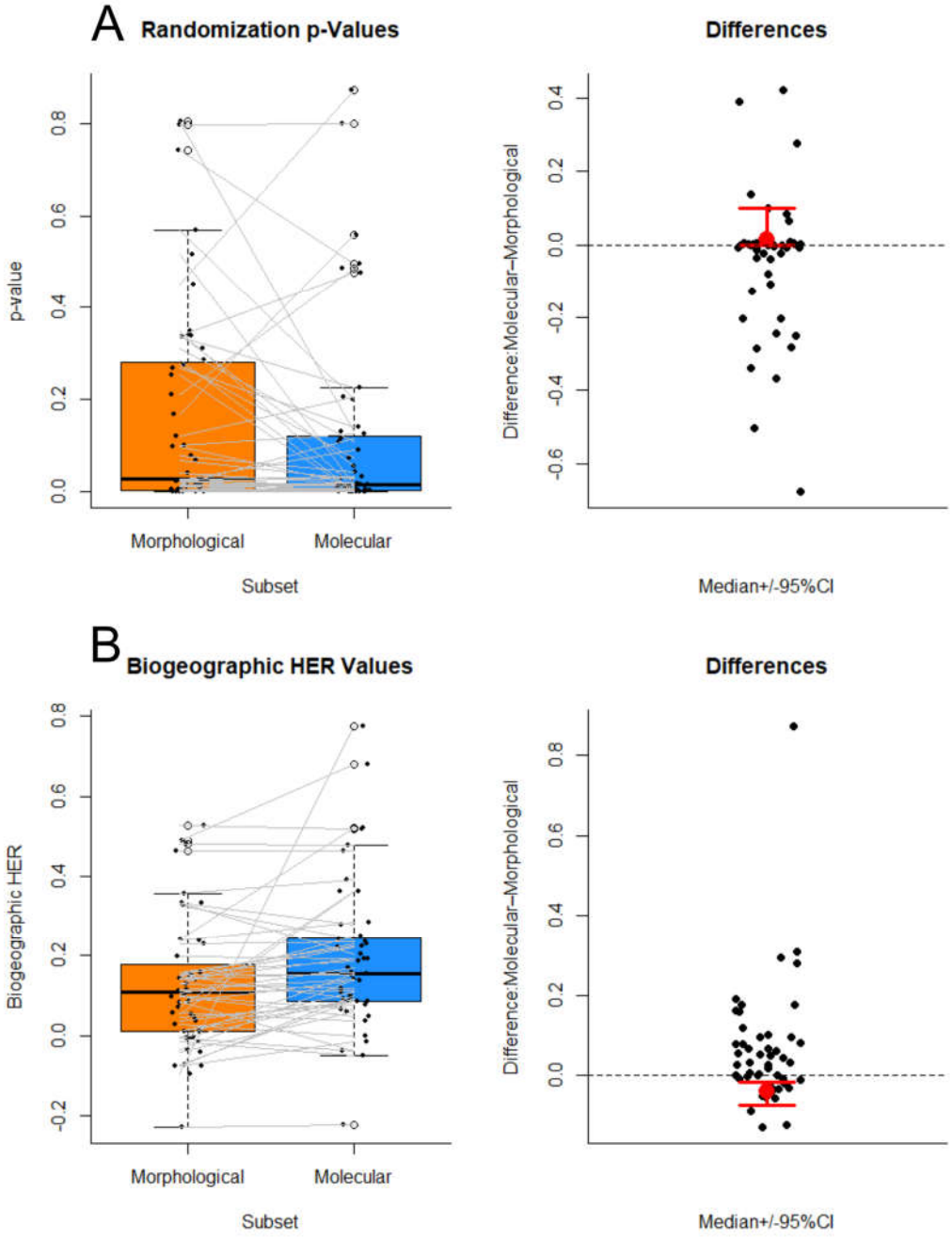

Fig. 4.5 Boxplots of raw values and differences in values between morphological and molecular trees for **A:** P-values for the CI/RI randomizations (V = 662, p =0.104) and **B:** Biogeographic HER (V = 288, p =0.002). Boxes delimit the upper and lower quartiles of the data, while central bars are median values. Whiskers delimit plus or minus 1.5 times the inter-quartile range, from the first and third quartiles. Grey lines connect pairs of values from the same clade. Differences given are molecular values minus morphological, with positive differences indicating higher values in the molecular subsample. In the null case, difference values would be randomly distributed around the estimated pseudomedian shown in red, with upper and lower 95% confidence intervals.

Binomial tests (**Table 4.10**) supported the results from the Wilcoxon tests, showing that selecting the tree for each clade with the highest fit metric value resulted in a significantly larger sample of molecular trees than expected by chance. Biogeographic HER showed a significant difference across the whole dataset (**Fig. 4.6**, panel D: success p-value = 0.688, binomial p-value = 0.013). While the difference in sample size was not significant for CI and RI across the whole sample, removing clades in which both trees had identical values did produce a significant result for both CI (**Fig. 4.6**, panel A: success p-value = 0.659, binomial p-value = 0.049) and RI (Figure 5, panel B: success p-value = 0.682, binomial p-value = 0.020). Significant differences were also found when considering only CI (success p-value = 0.667, binomial p-value = 0.014) and RI values (success p-value = 0.719, binomial p-value = 0.005) which deviated from the expected null. Interestingly, the number of clades selected using the randomized p-values was approximately the same for morphological and molecular trees, regardless of whether the whole dataset or only clades with significant p-values were considered (**Fig. 4.6**, panel C).

Dataset	Metric	Sample Size	Morphology Higher	Success p-value	Molecular Higher	Success p-value	Binomial p-value
Whole Dataset	CI	48	15	0.313	29	0.604	0.193
	RI	48	14	0.292	30	0.625	0.111
	p-Val	48	20	0.417	25	0.521	0.885
	HER	48	15	0.313	33	0.688	0.013
All Cases With Difference	CI	44	15	0.341	29	0.659	0.049
	RI	44	14	0.318	30	0.682	0.020
	p-Val	45	20	0.444	25	0.556	0.552
	HER	48	15	0.313	33	0.688	0.013
Either fit sig different from random	CI	33	9	0.273	22	0.667	0.014
	RI	32	7	0.219	23	0.719	0.005
	p-Val	33	13	0.394	17	0.515	0.999
Either fit sig different from random + one fit better than the other	CI	31	9	0.290	22	0.710	0.029
	RI	30	7	0.233	23	0.767	0.005
	p-Val	30	13	0.433	17	0.567	0.585

Table 4.10 Results of binomial tests for the number of cases molecular trees are selected over morphological trees based on the following measures of biogeographic fit: Consistency Index (CI), Retention Index (RI), CI/RI randomization p-values (p-Val) and Biogeographic Homoplasy Excess Ratio (HER). Tests were carried out on the whole dataset, only those datasets where there was a difference in fit values, only those datasets in which at least one of the CI or RI values significantly differed from a distribution of 10,000 randomisations and only those datasets in which at least one of the CI or RI values significantly differed from a distribution of 10,000 randomisations and there was a difference in fit value. Statistically significant results are highlighted in green.

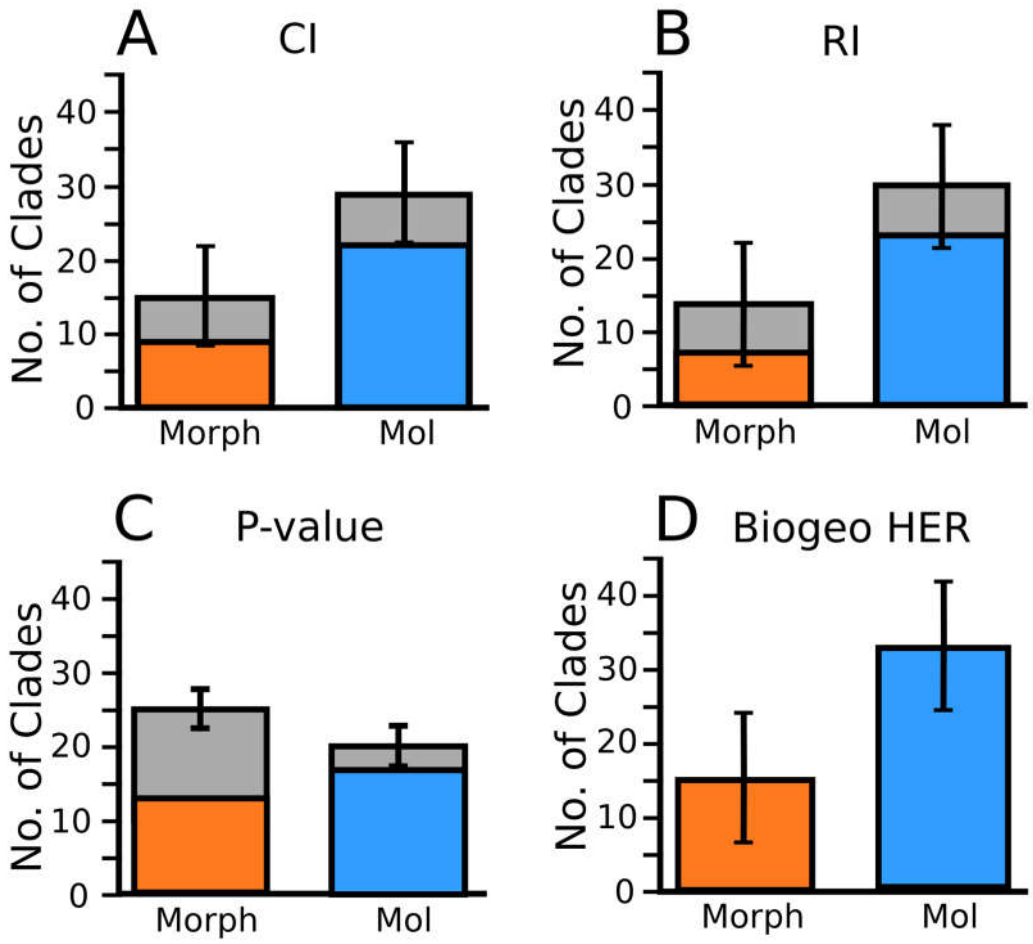

Fig. 4.6 Comparison of the number of trees in each sample (morphological or molecular) with a greater biogeographic fit than its counterpart. Bars show the number of clades in each subset, with binomial confidence intervals calculated using the approach of Clopper and Pearson (1934). **A:** Consistency Index, grey bars show totals for the whole sample, coloured bars indicate totals in the subset significantly different from the expected null (randomized p-value <0.05). **B:** Retention Index, grey bars show totals for the whole sample, coloured bars indicate totals in the subset significantly different from the expected null (randomized p-value <0.05). **C:** CI/RI randomization p-values, where grey bars show totals for the whole sample, coloured bars are clades with values <0.05 **D:** Biogeographic HER, counts are for the whole dataset.

4.3.4 Examples Of How Region Characters Map Onto Phylogenetic Trees

While CI, RI and Biogeographic HER generally show higher values on molecular trees, region characters were found to map onto morphological and molecular trees in a number of different ways. In many cases, the fit of region characters onto the molecular tree, but not the morphological one, was significantly higher than the expected null, even when values (especially for Biogeographic HER) were quite low. In a classic example of phylogeny echoing biogeography, the placental mammal dataset (**Fig. 4.7**) shows that biogeographic congruence is significantly greater for the molecular tree as groups with a cosmopolitan distribution, as well as those endemic to Africa and the Americas are located close to each other, resulting in higher fit metric values. *Epicrates* boas (**Fig. 4.8**) are another group where only the molecular tree shows biogeographic congruence significantly greater than the random null. In this case fit metric values are much higher, likely due to the smaller number of regions and the fact that there are no cosmopolitan species (species are generally found in only one region). Higher congruence on the molecular tree is due primarily to endemic Bahama and Puerto Rico clades only being supported on this phylogeny.

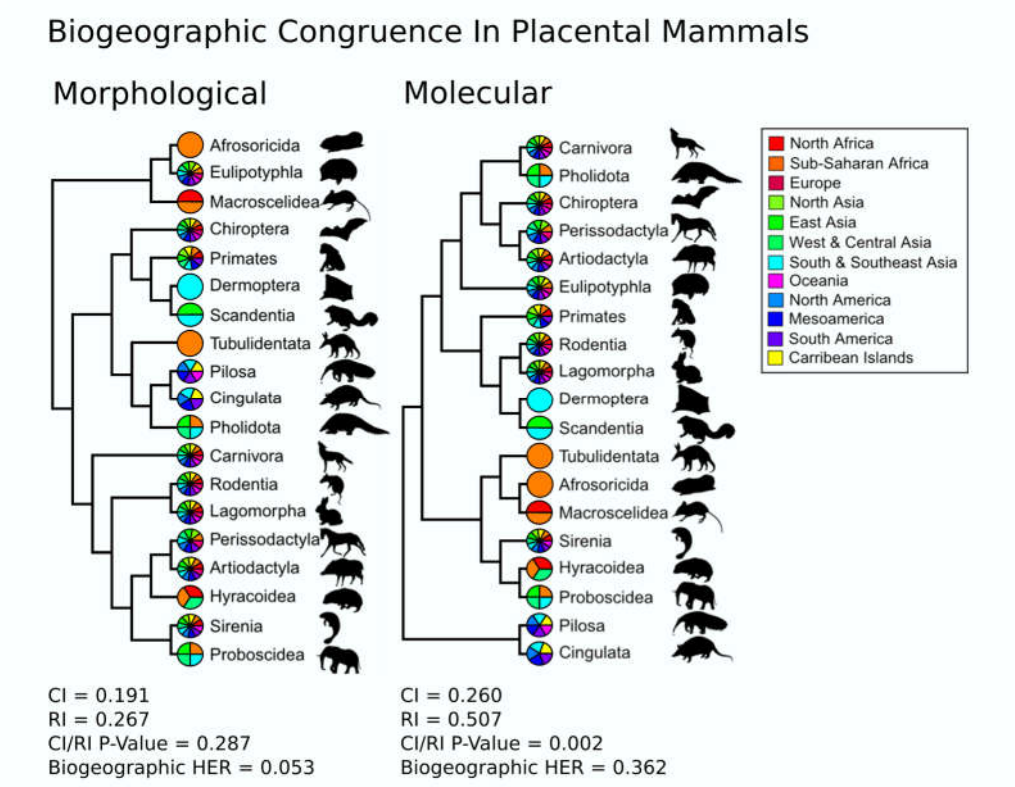

Fig. 4.7 Region characters mapped onto phylogenetic trees for placental mammals (Eutheria). Regions coded as present are shown as pie slices for each terminal taxon. Morphological and molecular trees are from O'Leary et al. 2013.

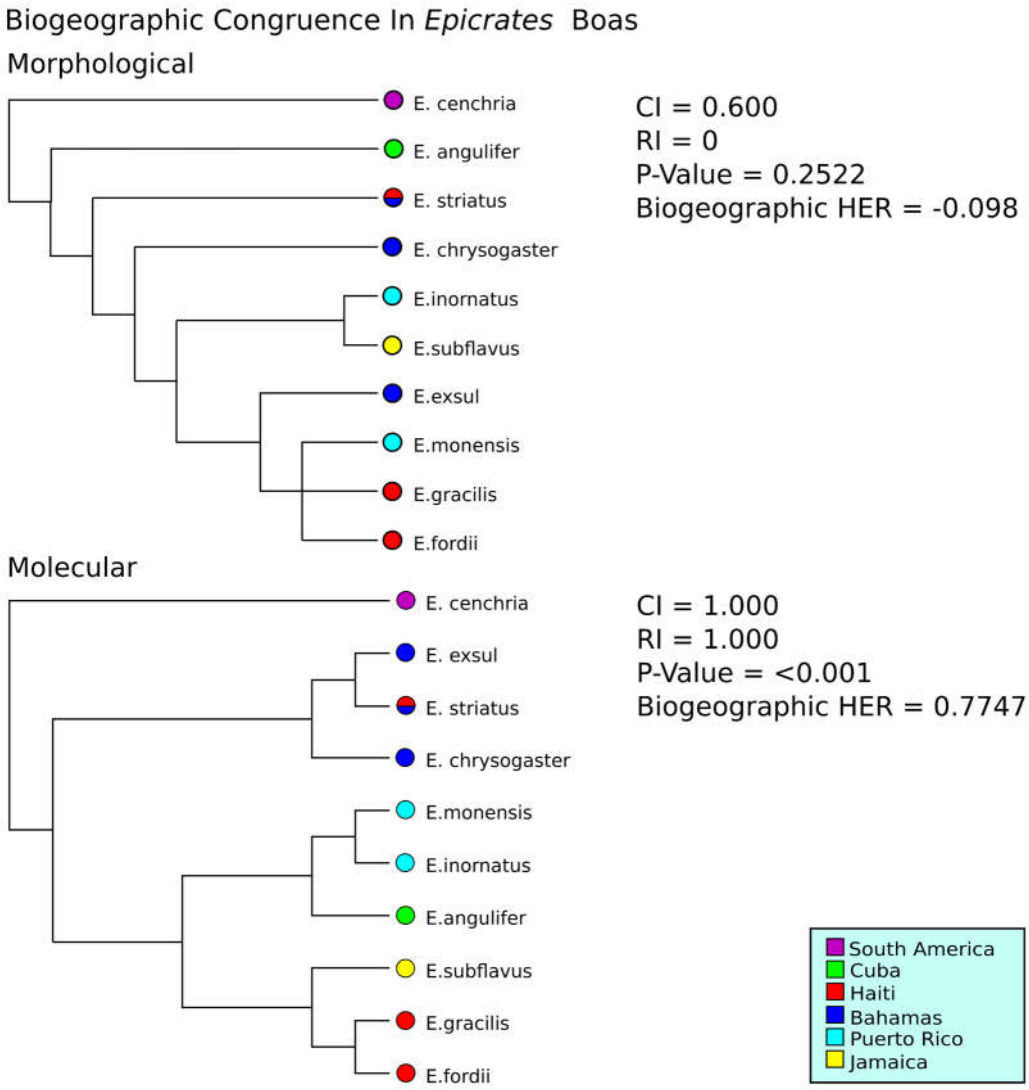

Fig. 4.8 Region characters mapped onto phylogenetic trees for boas of the genus *Epicrates*. Regions coded as present are shown as pie slices for each terminal taxon. Morphological tree is from Kluge 1989, molecular tree is from Tolson 1987.

It was not uncommon for both trees to show better region character fit than the expected null, although in most of these cases fit metric values were still higher for the molecular tree. In Caribbean anoles (**Fig. 4.9**) fit metric values are low, but still better than expected given the high number of taxa and regions in the trees. The molecular tree still shows higher values, particularly for Biogeographic HER, largely due to higher clustering of Puerto Rican, Cuban, Dominican and Colombian species. Diprotodontid marsupials (**Fig. 4.10**) show a similar pattern with higher fit values: both trees show congruence significantly greater than random. In this case, the difference in fit values is likely due to differences in tree shape, while both trees show near identical clustering of regions on the tips, more nested clades on the molecular tree results in higher fit metric values.

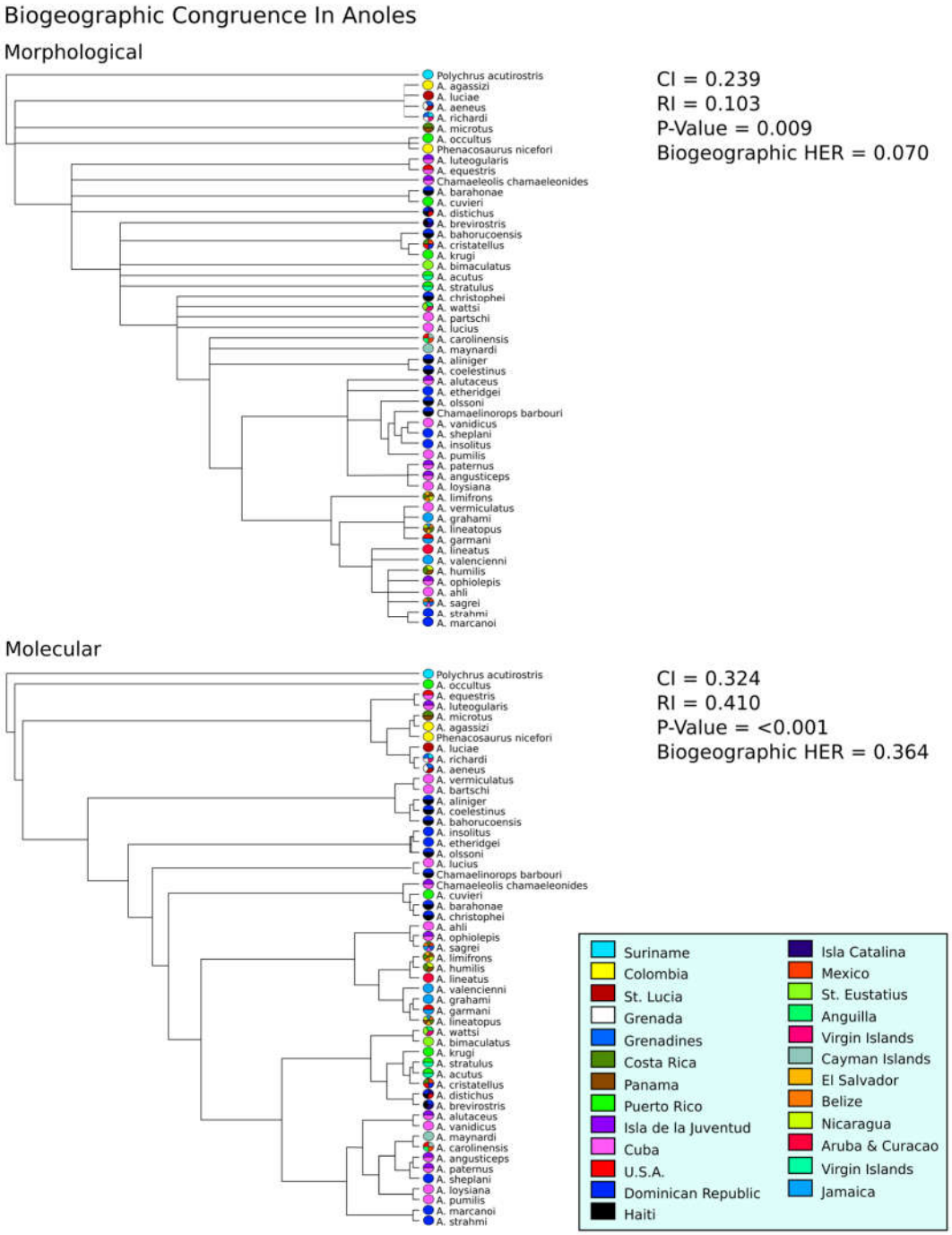

Fig. 4.9 Region characters mapped onto phylogenetic trees for lizards of the genus *Anolis*. Regions coded as present are shown as pie slices for each terminal taxon. Both the morphological and molecular trees are from Jackman 1999.

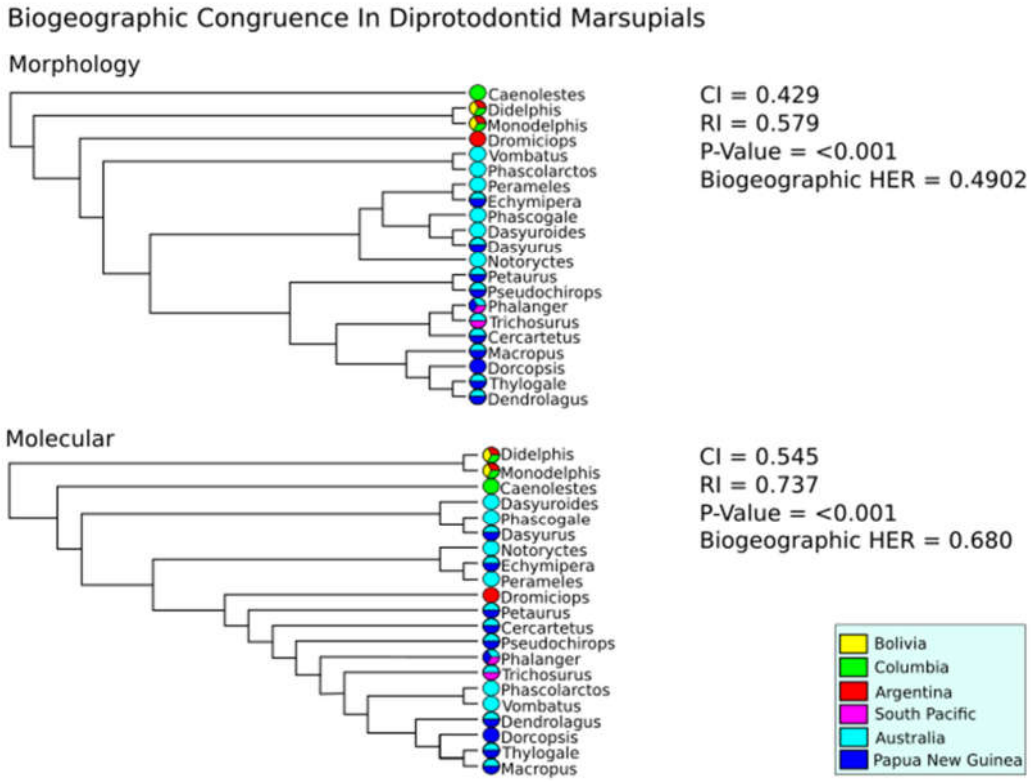

Fig. 4.10 Region characters mapped onto phylogenetic trees for diprotodontid marsupials (Diprotodontia). Regions coded as present are shown as pie slices for each terminal taxon. The morphological tree is from Horovitz et al. 2003, the molecular tree is from Meredith 2009.

In a minority of cases, neither tree shows greater biogeographic congruence than the expected null. In new world monkeys (**Fig. 4.11**), endemic genera (largely located in Brazil) are scattered fairly evenly across the tree and interspersed with highly cosmopolitan genera, such as the tamarins (*Saguinus*) and the night monkeys (*Aotus*). Unsurprisingly, fit metric values are relatively low and non-significant for both trees. Few clades showed significantly greater congruence for the morphological tree, but one such clade was the pine family (**Fig. 4.12**). While both trees showed congruence greater than the random null, both CI and Biogeographic HER (but not RI) were higher on the morphological tree, although this difference was slight. The slight improvement in fit values on this tree is likely due to the clustering together of a few Vietnamese and Chinese taxa, with the placement of the dawn redwood (*Metasequoia)*, *Taxodium* and *Glyptostrobus* together on the morphological tree.

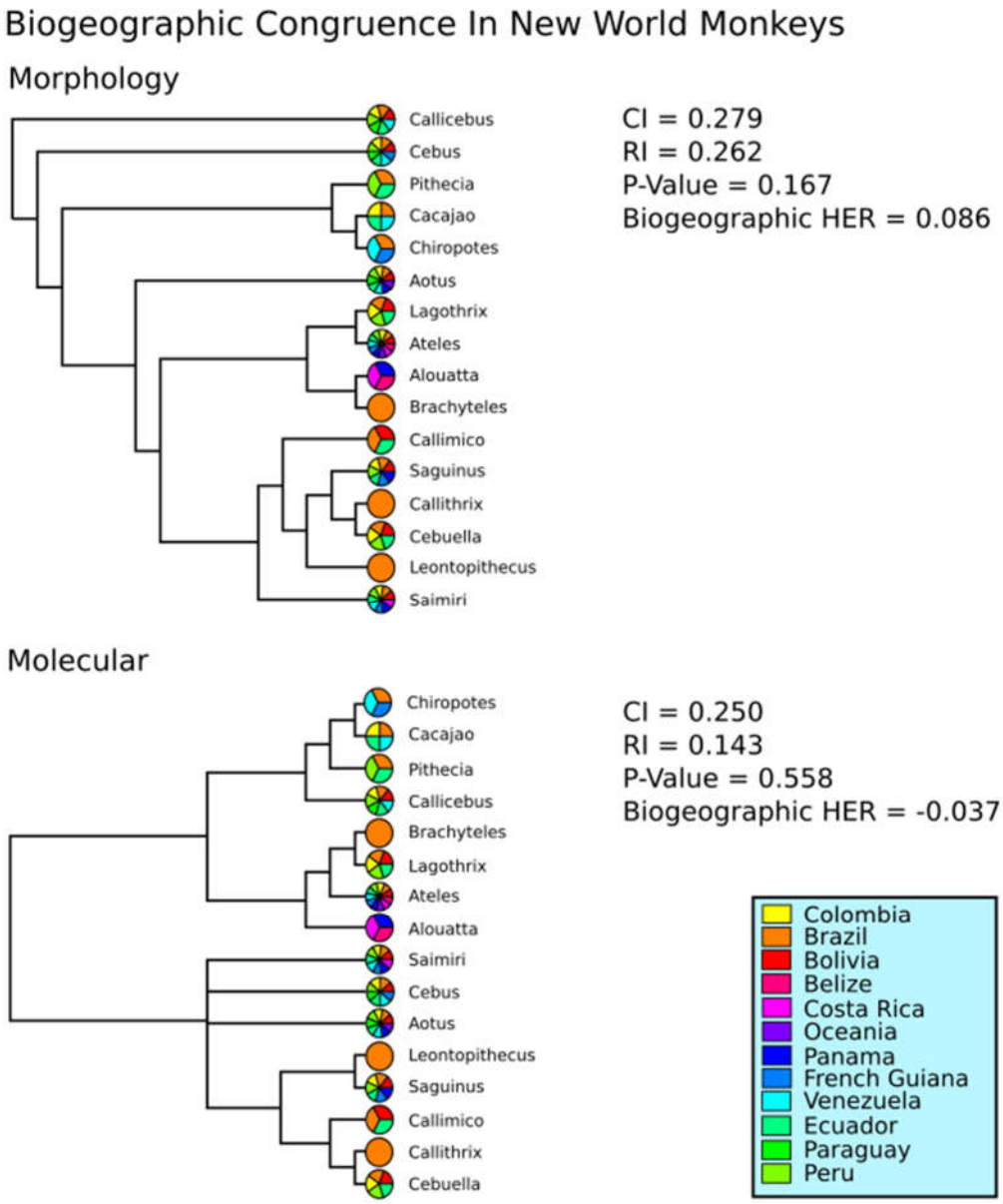

Fig. 4.11 Region characters mapped onto phylogenetic trees for new world monkeys (Ceboidea). Regions coded as present are shown as pie slices for each terminal taxon. The morphological tree is from Kay 1990, the molecular tree is from Schneider 1993.

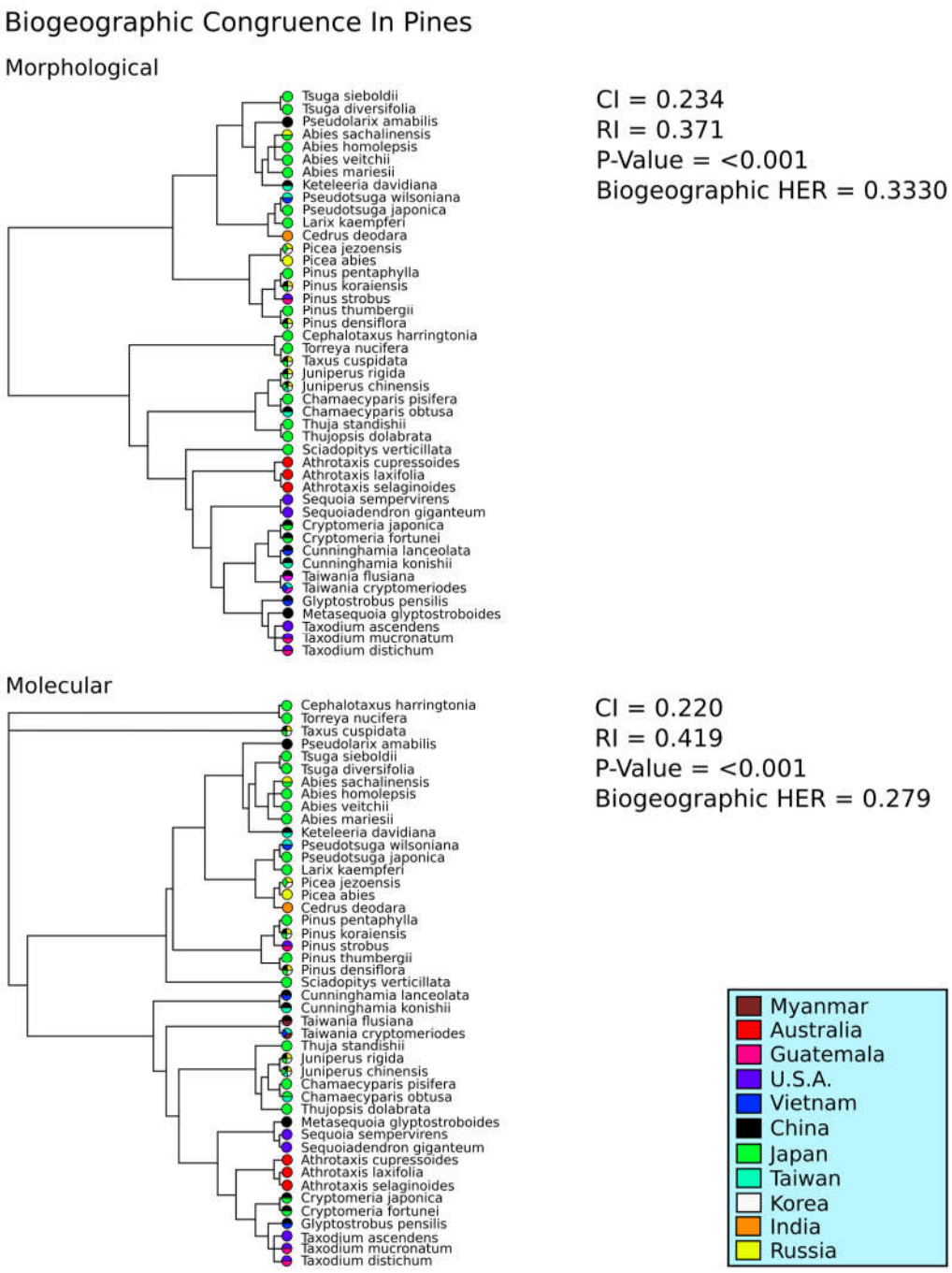

Fig. 4.12 Region characters mapped onto phylogenetic trees for the pine family (Pinaceae). Regions coded as present are shown as pie slices for each terminal taxon. The morphological tree is from Klymiuk 2012, the molecular tree is from Wang 2000.

4.3.5 Stratigraphic Congruence

Of the 22 clades analysed, 21 of them were from the vertebrates and 1 clade from plants. Of the vertebrate clades, 16 were mammal, 4 reptile and 1 bird (**Table 4.11**). The known age ranges of these clades, expressed in terms of the number of geological intervals the fossil record spans (Standard Range Length, SRL) varied between 16 and 879 intervals, with a mean of 157 and a median of 97. Minimum possible ghost ranges on trees (G_{min}) ranged between 2 and 41 (mean = 13, median = 11) while the maximum (G_{max}) varied between 22 and 1704 intervals (mean = 239, median = 140). The total sum of ghost ranges on the trees (Minimum Implied Gap, MIG) also varied considerably from as low as 4 to as high as 814 (mean = 114, median = 58), although MIGs of morphological (mean = 115, median = 61) and molecular (mean = 114, median = 55) were similar.

From the stratigraphic congruence metrics, the Stratigraphic Consistency Index (SCI) ranged between 0.2 and 0.846, with a mean of 0.562 and a median SCI of 0.55. SCI values of morphological (mean = 0.540, median = 0.515) and molecular (mean = 0.573, median = 0.561) trees were very similar and relatively high. Relative Completeness Index percentages (RCI %) were somewhat lower, ranging from -175 to 87.5% (mean = 22.257%, median = 43.538%). RCI differences between morphological (mean = 19.605%, median = 28.943%) and molecular (mean = 24.116, median = 44.505) trees were greater than for SCI, although still similar. Modified Manhattan Stratigraphic Measure (MSM*) values varied greatly, with the lowest reported value being 0.032 and the highest value being 1.0. Despite a great range of values, most values were relatively low (mean = 0.215, median = 0.174) and comparing the averages of morphological (mean = 0.218, median = 0.17) and molecular (mean = 0.215, median = 0.193) revealed MSM* values were similar for each subset.

Of the different versions of the Gap Excess Ratio employed, the simplest measure (Gap Excess Ratio, GER) showed both the lowest average values (mean = 0.566, median = 0.587) and the smallest range (0.151 to 1.0). GER values for the morphological (mean = 0.571, median = 0.581) and molecular trees (mean = 0.563, median = 0.587) were also very similar. The Topological Gap Excess Ratio (GERt) also showed very little difference between morphological (mean = 0.690, median = 0.636) and molecular (mean = 0.672, median = 0.686) trees, although values overall were higher (between 0.053 and 1.254, mean = 0.684, median = 0.667). Lastly, the Modified Gap Excess Ratio (GER*) values were highest of the three (between 0.087 and 1.0, mean = 0.750, median = 0.828), but again, there was almost no difference in stratigraphic fit between the samples of morphological (mean = 0.747, median = 0.828) and molecular (mean = 0.750, median = 0.820) trees. Values for all three metrics and especially GER*, were generally high, indicating the trees of most clades fitted their known fossil records well.

Clade	Category	SRL	MIG	Gmin	Gmax	GER	GERt	GER*	RCI (%)	SCI	MSM*
Chiroptera 1	Morph	96	46	10	94	0.571	0.810	0.992	52.083	0.588	0.217
	Mol	96	53	10	94	0.488	0.717	0.929	44.792	0.647	0.189
Chiroptera 2	Morph	235	118	18	161	0.301	0.455	0.565	49.787	0.545	0.153
	Mol	235	120	18	161	0.287	0.481	0.577	48.936	0.550	0.150
Phyllostomid Bats 1	Morph	24	66	11	207	0.719	0.534	0.613	-175.000	0.684	0.167
	Mol	24	44	11	207	0.832	0.678	0.905	-83.333	0.737	0.250
Phyllostomid Bats 2	Morph	68	52	4	216	0.774	0.882	0.997	23.529	0.783	0.077
	Mol	68	64	4	216	0.717	0.706	0.922	5.882	0.696	0.063
Megachiroptera	Morph	16	16	2	72	0.800	1.000	1.000	0.000	0.833	0.125
	Mol	16	22	2	72	0.714	0.792	0.995	-37.500	0.762	0.091
Chrysochloridae	Morph	58	24	6	50	0.591	0.806	0.999	58.621	0.563	0.250
	Mol	58	24	6	50	0.591	0.750	0.996	58.621	0.688	0.250
Glires	Morph	147	84	14	161	0.524	0.598	0.829	42.857	0.500	0.167
	Mol	147	82	14	161	0.537	0.605	0.838	44.218	0.550	0.171
Phrynostomatidae	Morph	335	53	12	145	0.692	1.097	0.708	84.179	0.842	0.226
	Mol	335	55	12	145	0.677	1.145	0.708	83.582	0.816	0.218
Plectonine Bats	Morph	28	10	5	22	0.706	0.667	0.990	64.286	0.500	0.500
	Mol	28	12	5	22	0.588	0.667	0.959	57.143	0.500	0.417
Mormoopidae	Morph	32	4	5	28	1.000	1.000	0.990	87.500	0.846	1.000
	Mol	32	4	5	28	1.000	1.000	0.990	87.500	0.846	1.000
Arctoidea	Morph	154	62	17	135	0.619	0.635	0.826	59.740	0.400	0.274
	Mol	154	66	17	135	0.585	0.630	0.801	57.143	0.333	0.258
Talpidae	Morph	68	56	11	64	0.151	0.053	0.087	17.647	0.200	0.196
	Mol	68	46	11	64	0.151	0.053	0.087	17.647	0.200	0.196
Macropodidae	Morph	47	35	6	122	0.326	0.303	0.620	25.532	0.429	0.171
	Mol	47	34	6	122	0.349	0.258	0.550	27.660	0.500	0.176
Didelphidae	Morph	220	89	11	275	0.705	1.254	0.550	59.545	0.674	0.124
	Mol	220	92	11	275	0.693	1.175	0.550	58.182	0.698	0.120
Echimyidae	Morph	31	48	10	122	0.705	1.254	0.550	59.545	0.674	0.124
	Mol	31	55	8	97	0.693	1.175	0.550	58.182	0.698	0.120
Erinaceidae	Morph	98	76	10	122	0.411	0.590	0.970	22.449	0.600	0.132
	Mol	98	42	10	122	0.714	0.946	1.000	57.143	0.700	0.238
Feliformia	Morph	154	372	12	482	0.234	0.421	0.356	-141.558	0.314	0.032
	Mol	154	370	12	482	0.238	0.358	0.243	-140.260	0.329	0.032
Pinales	Morph	879	814	41	1704	0.535	0.636	0.895	7.395	0.443	0.050
	Mol	879	814	41	1704	0.554	0.694	0.937	11.035	0.475	0.052
Squamata	Morph	397	117	31	192	0.466	0.522	0.910	70.529	0.529	0.265
	Mol	397	137	31	192	0.342	0.276	0.506	65.491	0.412	0.226
Ratites	Morph	63	60	12	93	0.466	0.522	0.460	4.762	0.364	0.200
	Mol	63	53	12	93	0.342	0.276	0.760	15.873	0.455	0.226
Crocodilia	Morph	138	124	21	345	0.682	0.809	0.988	10.145	0.333	0.169
	Mol	138	101	21	345	0.753	0.874	0.998	26.812	0.571	0.208
Iguanidae	Morph	155	209	18	439	0.546	0.477	0.594	-34.839	0.484	0.086
	Mol	155	208	18	439	0.549	0.523	0.701	-34.194	0.452	0.087

Table 4.11 Summary metrics for the 44 phylogenetic trees included in the analysis of stratigraphic congruence. Columns are: Category (morphological or molecular), Standard Range Length (SRL), Minimum Implied Gap (MIG), minimum possible gap (G_{min}), maximum possible gap (G_{max}), Gap Excess Ratio (GER), Topological Gap Excess Ratio (GERt), Modified Gap Excess Ratio (GER*), Relative Completeness Index (RCI), Stratigraphic Consistency Index (SCI) and Modified Manhattan Stratigraphic Measure (MSM*).

Paired Wilcoxon signed-rank tests failed to detect any significant difference in the stratigraphic congruence of morphological and molecular trees according to any of the above metrics (**Table 4.12**), with the SCI being the closest to significant (V = 59.5, p-value = 0.159) showing difference values that were skewed to the positive relative to the pseudomedian (**Fig. 4.13**, panel A). The MSM* (**Fig. 4.13**, panel B) and both the GER and GER* (**Fig. 4.14**) showed difference values that appeared fairly evenly scattered around their pseudomedians.

Metric	**Wilcoxon Signed-Rank test statistic (V)**	**p-Value**
SCI	59.5	0.159
MIG	87	0.762
RCI	87	0.763
MSM*	102	0.486
GER	121	0.305
GERt	117	0.387
GER*	79	0.925

Table 4.12 Results of paired Wilcoxon signed-rank tests on the two data categories (Morphological & Molecular) for the following metrics: Stratigraphic Consistency Index (SCI), Minimum Implied Gap (MIG), Relative Completeness Index (RCI), Modified Manhattan Stratigraphic Measure (MSM*), Gap Excess Ratio (GER), Topological Gap Excess Ratio (GERt) and Modified Gap Excess Ratio (GER*).

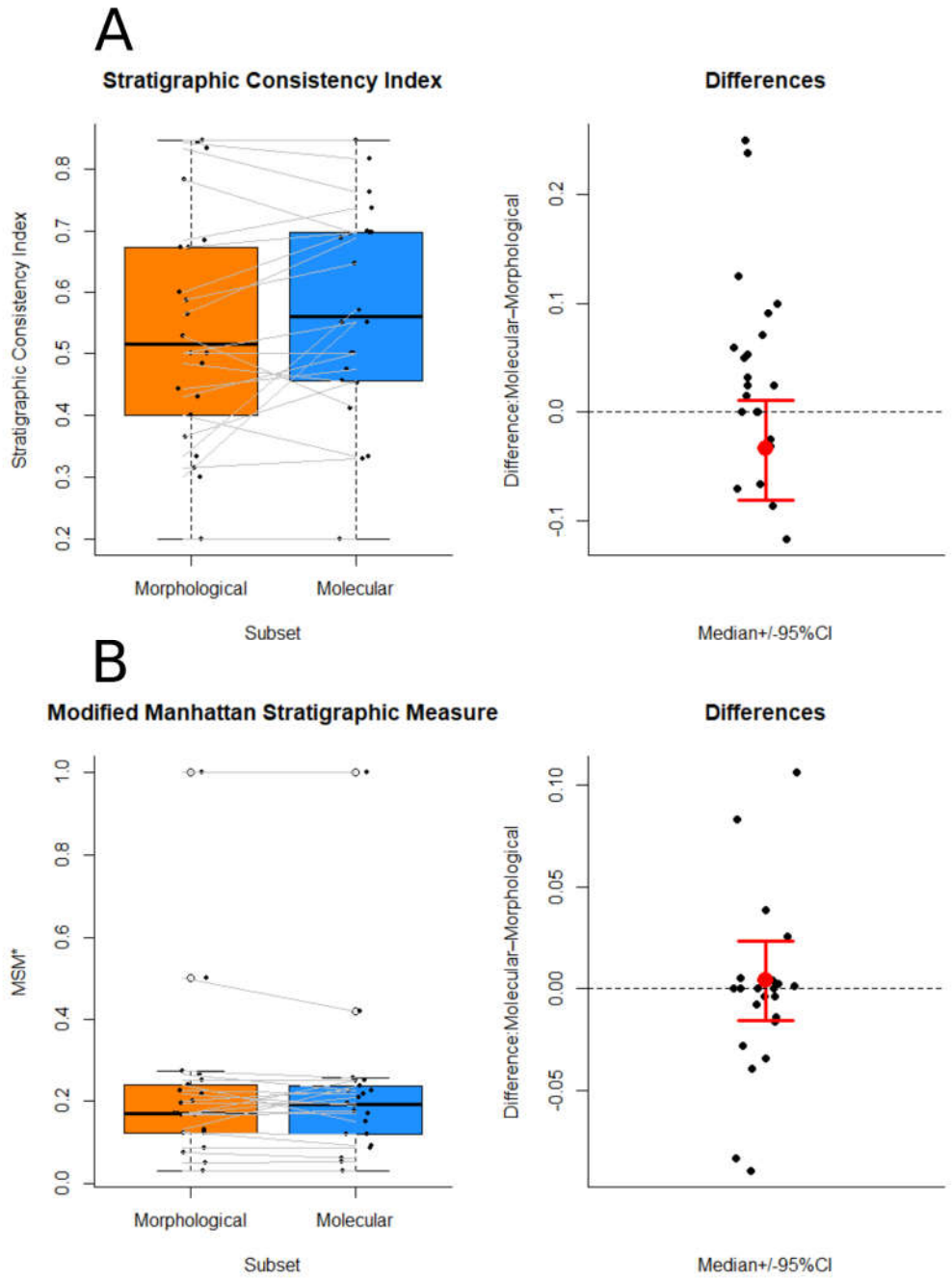

Fig. 4.13 Boxplots of raw values and differences in values between morphological and molecular trees for **A:** Stratigraphic Consistency Index (V = 59.5, p = 0.159) and **B:** Modified Manhattan Stratigraphic Measure (V = 102, p = 0.486). Boxes delimit the first and third quartiles of the data, while central bars are median values. Whiskers delimit plus or minus 1.5 times the inter-quartile range, from the first and third quartiles. Grey lines connect pairs of values from the same clade. Differences given are molecular values minus morphological, with positive differences indicating higher values in the molecular subsample. In the null case, difference values would be randomly distributed around the estimated pseudomedian shown in red, with upper and lower 95% confidence intervals.

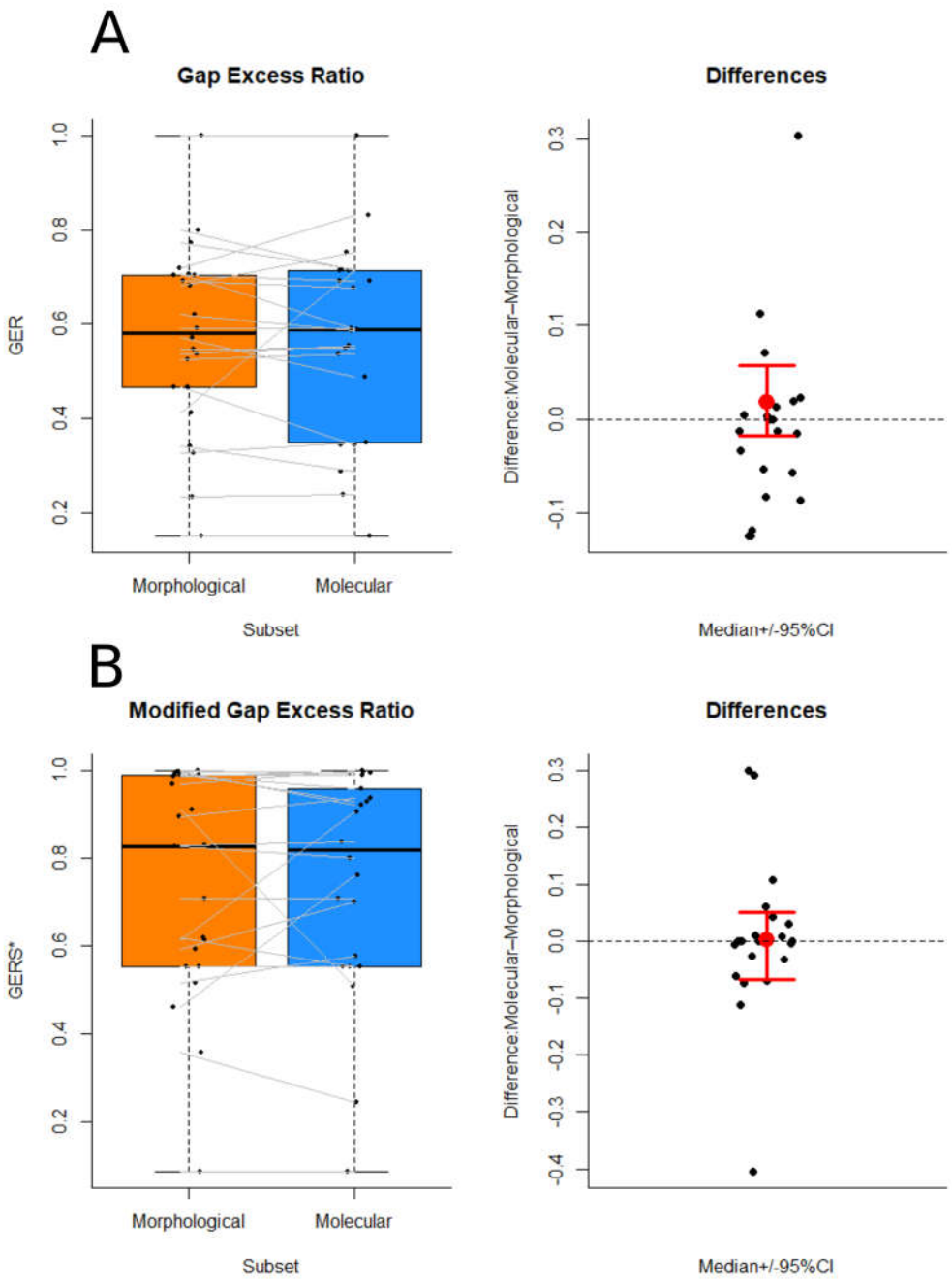

Fig. 4.14 Boxplots of raw values and differences in values between morphological and molecular trees for **A:** Gap Excess Ratio (V = 121, p = 0.305) and **B:** Modified Gap Excess Ratio (V = 79, p = 0.925). Boxes delimit the first and third quartiles of the data, while central bars are median values. Whiskers delimit plus or minus 1.5 times the inter-quartile range, from the first and third quartiles. Grey lines connect pairs of values from the same clade. Differences given are molecular values minus morphological, with positive differences indicating higher values in the molecular subsample. In the null case, difference values would be randomly distributed around the estimated pseudomedian shown in red, with upper and lower 95% confidence intervals.

Similarly, binomial tests showed that morphological and molecular trees were equally likely to be selected using best stratigraphic fit as a criterion (**Table 4.13**). While the sample of molecular trees selected using highest SCI as a criterion was slightly larger than the sample of morphological trees (**Fig. 4.15**, panel A), the highest MSM* criterion produced approximately equal counts in both subsets (**Fig. 4.15**, panel C). Selecting by highest GER (**Fig. 4.15**, panel B) and GER* (**Fig. 4.15**, panel D) actually resulted in slightly more morphological trees being selected than molecular. The inability to detect significant differences in stratigraphic congruences is likely in part due to a smaller sample size, as differences between many of the other metrics were also non-significant when Wilcoxon signed-rank tests were carried out (**Table 4.14**). While the number of phylogenetic characters was found to be significantly different in the smaller sample (V = 0, p-value = <0.001) the only biogeographic fit metric that showed a significant difference was the Biogeographic HER (V = 58, p-value = 0.025). None of the binomial tests using biogeographic fit metrics were significant for the smaller dataset (**Table 4.15**), although Biogeographic HER approached the 0.05 confidence level (p-value of success = 0.727, binomial p-value = 0.052).

Metric	Sample Size	Morphology Higher	Success p-value	Molecular Higher	Success p-value	Binomial p-value
SCI	22	6	0.273	13	0.591	0.524
MIG	22	10	0.455	10	0.455	0.832
RCI	22	9	0.409	10	0.455	0.832
MSM*	22	10	0.455	8	0.364	0.286
GER	22	11	0.5	8	0.364	0.286
GERt	22	11	0.5	8	0.364	0.286
GER*	22	10	0.455	7	0.318	0.134

Table 2.13 Results of binomial tests for the number of cases molecular trees are selected over morphological trees based on the following measures of stratigraphic fit: Stratigraphic Consistency Index (SCI), Minimum Implied Gap (MIG), Relative Completeness Index (RCI), Modified Manhattan Stratigraphic Measure (MSM*), Gap Excess Ratio (GER), Topological Gap Excess Ratio (GERt), Modified Gap Excess Ratio (GER*).

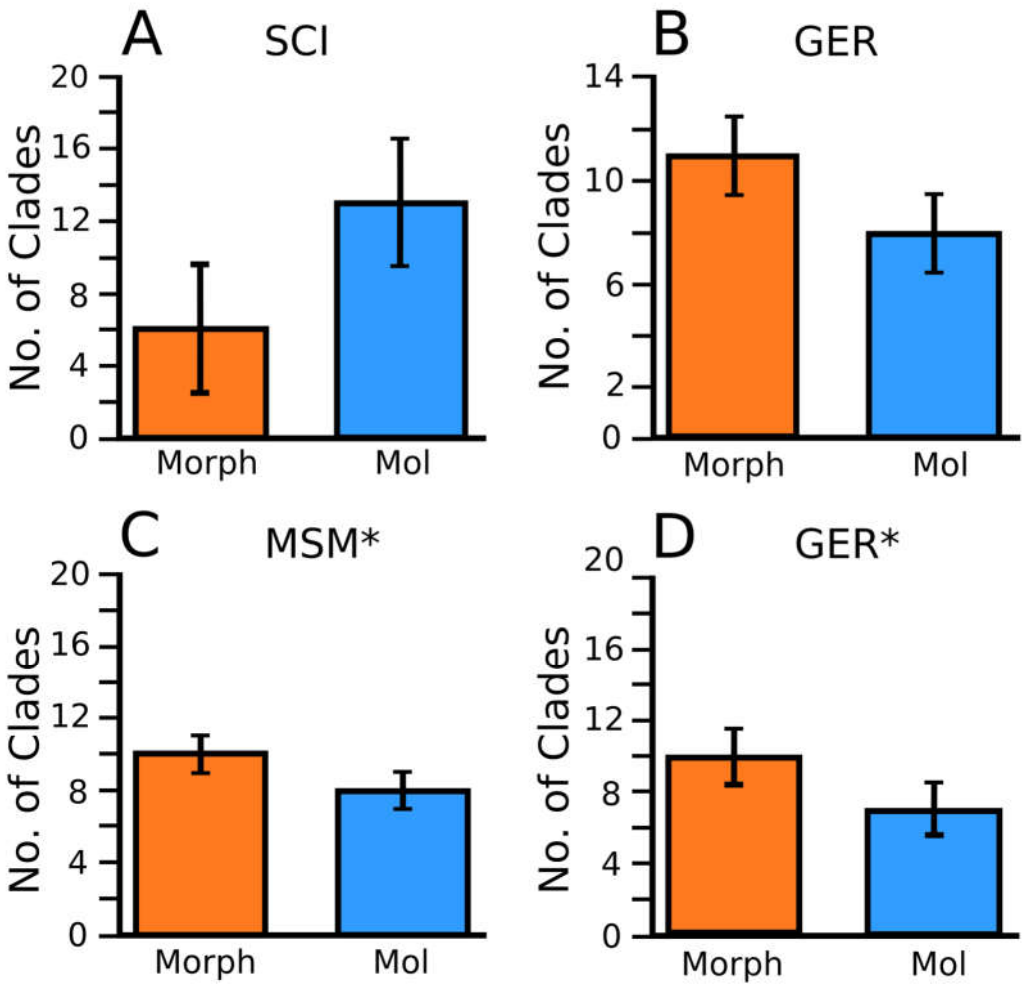

Fig. 4.15 Comparison of the number of trees in each sample (morphological or molecular) with greater stratigraphic fit. Bars show the number of clades in each subset, with binomial confidence intervals calculated using the approach of Clopper and Pearson (1934). **A:** Stratigraphic Consistency Index (SCI), **B:** Gap Excess Ratio (GER), **C:** Modified Manhattan Stratigraphic Measure (MSM*), **D:** Modified Gap Excess Ratio (GER*).

Metric	Wilcoxon Signed-Rank test statistic (V)	p-Value
Publication Year	2.5	0.115
Phylogenetic Characters	0	<0.001
I*m*	128	0.677
CI	72	0.135
RI	76	0.175
p-value	138	0.225
Biogeographic HER	58	0.025

Table 4.14 Results of paired Wilcoxon signed-rank tests testing morphological and molecular trees used in the stratigraphic congruence analysis study. Tests were carried out for the following metrics: publication year, number of phylogenetic characters, Heard's Index of tree balance (I*m*), Consistency Index (CI), Retention Index (RI), probability of CI & RI values falling within the null distribution (CI/RI Randomization p-value) and Homoplasy Excess Ratio (Biogeographic HER). Statistically significant results are highlighted in green.

Dataset	Metric	Sample Size	Morphology Higher	Success p-value	Molecular Higher	Success p-value	Binomial p-value
Whole Dataset	CI	22	8	0.364	13	0.591	0.524
	RI	22	7	0.318	14	0.636	0.286
	p-Val	22	11	0.5	9	0.409	0.524
	HER	22	6	0.273	16	0.727	0.052
All Cases With Difference	CI	21	8	0.381	13	0.619	0.383
	RI	21	7	0.333	14	0.667	0.189
	p-Val	20	11	0.550	9	0.450	0.824
	HER	22	6	0.273	16	0.409	0.524
Either fit sig different from random	CI	16	6	0.375	9	0.563	0.804
	RI	16	5	0.313	10	0.625	0.455
	p-Val	15	6	0.4	7	0.467	0.999
Either fit sig different from random + one fit better than the other	CI	15	6	0.4	9	0.6	0.607
	RI	15	5	0.333	10	0.667	0.302
	p-Val	13	6	0.462	7	0.538	0.999

Table 4.15 Results of binomial tests for the number of cases molecular trees are selected over morphological trees used in the stratigraphic congruence analysis study, based on the following measures of biogeographic fit: Consistency Index (CI), Retention Index (RI), CI/RI randomization p-values (p-Val) and Biogeographic Homoplasy Excess Ratio (HER). Tests were carried out on the whole dataset, only those datasets where there was a difference in fit values, only those datasets in which at least one CI or RI values significantly differed from a distribution of 10,000 randomisations and only those datasets in which at least one of the CI or RI values significantly differed from a distribution of 10,000 randomisations and there was a difference in fit value.

4.4. Discussion

By compiling biogeographic data and summarising it in the form of region presence/absences, it was found that the distributions of extant taxa were significantly more congruent with phylogeny than expected by chance for most clades. Biogeographic data, therefore, seems to contain a phylogenetic signal, even in clades not typically regarded as having strong phylogeographic patterns. Secondly, congruence values were found to be significantly higher for molecular topologies when compared to alternative hypotheses of relationships inferred using morphological data. As biogeographic congruence metrics showed a significant positive correlation with both publication year and the number of phylogenetic characters used to produce the tree, it seems likely that how well region presence/absence characters fit onto a tree is a genuine test of phylogenetic support, rather than being strongly influenced by other factors. This supports the assertion that molecular trees are more reliable than morphological trees, probably due to morphological traits evolving convergently in different geographic regions.

4.4.1 Biogeography Is Underutilised In Tests Of Phylogeny

4.4.1.1 Phylogeny & Historical Biogeography

While scientists in a wide range of fields have been interested in quantifying or describing biogeographic patterns, studies of historical biogeography have focused on using area cladograms to reconstruct the relationships between biotas (Nelson and Platnick 1981; Morrone and Crisci 1995). More recently, model based methods which infer ancestral regions from a phylogeny using maximum likelihood or Bayesian approaches have become popular (Buerki et al. 2011; Matzke 2014; Yu et al. 2015) . Studies of biogeography have largely focused on distinguishing between dispersal and vicariant mechanisms of speciation (Zink et al. 2000; Sanmartín 2003; Luebert et al. 2017), or the importance of long distance dispersal (Raxworthy et al. 2002; de Queiroz 2005; Zhou et al. 2006) rather than studying the ecological and evolutionary drivers of large-scale biogeographic patterns (Wiens and Donoghue 2004; Velasco 2018). To summarise, nearly all existing phylobiogeographic methods use phylogeny as a means of developing and testing biogeographic hypotheses. The analyses in this chapter take a novel approach, using biogeography as an independent test of phylogenetic hypotheses in a diverse sample of clades. Surprisingly, the distributions of most clades showed a phylogenetic signal which was stronger than the expected random null. Although clades with wide taxon ranges (e.g. groups that migrate or fly) are often assumed to be more prone to long distance dispersal, there was little evidence of a correlation between

taxonomic affinity or taxon ranges and biogeographic congruence values. While many of the clades with highest biogeographic congruence did have relatively restricted distributions, some clades that might be expected to show a clear phylogenetic signal in their distribution in fact showed a poor fit between the two. Examples include mammal groups such as the dog family (Canidae) and new world monkeys (Ceboidea), scaled reptiles (Squamata) and plant groups such as dwarf dandelions (*Krigia*) and cypresses (Cupressaceae). Conversely, some groups that might be expected to have weak biogeographic signal, including bats and ducks actually showed relatively high congruence. These results are in agreement with empirical studies which show that dispersal ability and range size are not directly correlated (Lester et al. 2007), with dispersal ability being strongly interdependent on multiple life history traits (Comte and Olden 2018).

4.4.1.2 Repurposing Data For Phylogenetic Tests

The results of this chapter support the widespread use and incorporation of biogeographic data as a means of testing the robustness of phylogenies. Practically speaking, there are a number of difficulties to overcome regarding the marriage of phylogenetic and biogeographic information. Firstly, much of the distributional data available for this study was species occurrence data, while phylogenetic studies rarely sample taxa evenly or comprehensively at the level of species (Hillis and Cannatella 1998; Heath et al. 2008). Limitations on the time and cost available to dedicate to phylogenetic research (Cummings and Meyer 2005), as well as the difficulties of inferring relationships between highly similar taxa (Parks et al. 2009) mean that while sampling techniques are improving (Agnarsson et al. 2010; Pyron and Wiens 2011; Vélez-Zuazo and Agnarsson 2011; Pyron et al. 2013), most research effort is still focused on discerning relationships at the level of genera, families and orders. A further problem is that phylogenetic analyses from different authors, or using different sources of data, rarely use identical sets of taxa, necessitating taxon pruning which results in a less well resolved tree. As a result, the majority of phylogenies that were analysed in this chapter contained genera or families as terminal taxa. That biogeographic regions still mapped onto these trees significantly better than expected due to chance agrees with previous studies showing that there is a phylogenetic signal in the distributions of clades of higher taxonomic rank (Williams et al. 1997), despite most biogeographic studies focusing on species (Araújo and Guisan 2006; Brown 2009). Currently, compiling and amalgamating species occurrences so that they can be applied to higher taxonomic ranks is a significant time investment but could conceivably be automated to a degree, allowing vast amounts of existing occurrence data to be used to test phylogenies.

The main factor limiting widespread application of this approach are biases in the phylogenetic and biogeographic data available for different clades of organisms. Many of the clades analysed were reptile or mammal groups and this is almost entirely due to the availability of existing data. Clades of fish, plants and invertebrates have received proportionally less research effort given their high levels of taxonomic diversity (Sanderson 2008; Thomson and Shaffer 2010). Even within more speciose groups, sampling and research effort is often highly uneven (Heath et al. 2008; Reddy 2014). There are often group-specific biases in the types of phylogenetic data or analyses used (Wortley and Scotland 2006; Willis et al. 2007; Rota-Stabelli et al. 2011) and, while this may be a reflection of the practical utility of different sources of information depending on a specific groups' physiology or ecology, it makes the comparison of phylogenies based on different sources of information (e.g. morphological and molecular) difficult.

Data on species distribution is arguably even more strongly biased towards certain clades. Endangered or charismatic clades of birds and mammals are often the target of conservation programs or assessments of taxonomic diversity (Cardoso Da Silva and Bates 2002; Whittaker et al. 2005) which contribute significantly to biogeographic databases. Endangered clades are likely to have taxa with restricted ranges (Jones et al. 2003; Kiessling and Aberhan 2007), and, therefore, can require less sampling effort to accurately assess their biogeographic distribution than non-threatened clades with cosmopolitan taxa. Habitat can also bias sampling of taxa (Reddy and Dávalos 2003; Costa et al. 2010), as taxa present in large remote regions are likely to be less well sampled than taxa living in well populated or accessible areas. Sampling is also not necessarily equal for taxa of different body size, as small taxa (e.g. arthropods) are likely to be less well sampled simply because they require targeted, specific methods. Although methods of accounting for these biases when estimating species richness exist (Gotelli and Colwell 2011), they do not usually account for the failure to record specific taxa.

Uneven sampling makes patterns at finer spatial scales more prone to error. The impact of uneven spatial sampling was reduced somewhat in this study by testing fit of binary region characters with relatively coarse spatial resolution. This was a practical solution given the terminal taxa in many of the phylogenies were of higher taxonomic rank than the species for which biogeographic data was being recorded and helped with summarising the biogeography of taxa with large ranges in an easily codifiable form. This method can be applied to any group of organisms, regardless of phylogenetic affinity or ecology without detailed specific knowledge of a taxon's abundance or range but does result in less well resolved descriptions of ranges. Testing more case-specific phylogenetic and biogeographic mechanisms and patterns requires more accurate,

comprehensive sampling of species or subspecies as well as sufficiently well resolved phylogenies to map these distributional patterns onto.

4.4.2 Phylogeny and Biogeography Are Congruent

Region characters fit significantly better than expected onto most phylogenies, indicating taxon distributions are historically contingent to some degree. Although evolutionary history clearly influences the biogeography of clades, the link between the two only started to be appreciated relatively recently (Crisci et al. 2006; Warren et al. 2014) and is still overlooked in some studies (Barraclough and Vogler 2000; Webb et al. 2002). This is, in some ways, surprising considering the original formulations of the theory of evolution through natural selection by Darwin and Wallace were in a large part inspired by historical biogeography (Crisci and Katinas 2009). Historical biogeographic patterns can often be difficult to illuminate, as current species ranges are not necessarily indicative of their past ranges or those of their ancestors (Lynch 1989; Barraclough and Vogler 2000; Losos and Glor 2003) and obtaining data on species ancestral ranges (Springer et al. 2011) is often difficult. The difficulties of inferring historical patterns have led authors to focus instead on the role of climate in shaping biogeographic patterns at larger scales (Pearson and Dawson 2003; Ezard et al. 2011; Frainer et al. 2017).

Widespread congruence between phylogeny and the distributions of taxa suggests that, in addition to climate, biogeographic patterns are also a reflection of past diversification. This has been evident, albeit often on smaller spatial scales, from the phylogeographic literature (Avise et al. 1987; Bermingham and Moritz 1998; Taberlet et al. 1998; Caccone et al. 2002; Tolley et al. 2006). Environmental variation ensures that not only are ecological niches not evenly distributed but that some habitats or regions are more easily accessible than others. Geographical isolation, climatic change or tectonic events fragment and reshape regions, facilitating diversification (Wiley 1988; Upchurch et al. 2002; Luebert et al. 2017) as taxa develop novel morphologies and colonise vacant niches to escape competitors (Jeffires and Lawton 1984; Silvertown 2004). Studies of adaptive radiations (Guyer and Slowinski 1993; Schluter 2000) suggest that these processes are responsible for generating many of the diversity patterns we see in clades. While many of the most well studied and compelling examples are extremely rapid island radiations (Gillespie 2004; Givnish et al. 2009; Muschick et al. 2012), similar diversification patterns have now been shown at the continental scale in some cases (Hughes and Eastwood 2006) and over time scales orders of magnitude longer than rapid adaptive radiations (Burbrink and Pyron 2010; Jetz et al. 2012). Extinction events can also facilitate radiations, likely through the emptying of niches on a global scale (Toljagic and Butler 2013; Halliday et al. 2016). Compounded with the fact that it is now clear that several large clades diversified relatively recently (Schuettpelz and Pryer 2009;

Arakaki et al. 2011), perhaps it is not surprising that distributional patterns to some extent reflect recent evolutionary history.

4.4.3 Taxon Distributions Are More Congruent With Molecular Phylogenies Than With Morphological Alternatives

In this study, it was found that molecular phylogenies had significantly higher congruence values than morphological phylogenies of the same clade. While there was a general appreciation that biogeographic patterns can reflect the genetic relationships of molecular data, this study is the first to empirically identify such a pattern in a wide range of different clades. While the majority of phylogeographic studies focus on relatively small-scale patterns (Avise et al. 1998; Hewitt 2001), patterns of restricted distribution and endemism are also common at larger scales. In the famous example of placental mammals, it has been proposed that the widespread vacation of niches occupied by the dinosaurs in the wake of the K-Pg mass extinction could be responsible for numerous parallel adaptive radiations of major mammal groups into different regions (Murphy, Eizirik, Johnson, et al. 2001; O'Leary et al. 2013). Two major living groups of mammals (Laurasiatheria and Afrotheria) show geographically restricted parallel radiations which have convergently evolved a number of the same traits, both including insectivorous, aquatic and ungulate forms in both groups (Madsen et al. 2001). Eutherian mammals are not the only large clade to show evidence of these kinds of large-scale radiations as molecular phylogenies have illuminated similar patterns in modern birds (Jetz et al. 2012), amphibians (Bossuyt and Milinkovitch 2000) and plants (Cowling and Witkowski 1994; Lengyel et al. 2010). It has been shown that large phylogenies are significantly more unbalanced than expected if species diverge randomly (Guyer and Slowinski 1993), that is some clades are far more diverse than others in a manner consistent with adaptive radiations of select clades. These studies and the findings of this chapter support the idea that while patterns of diversification are geographically localised, novel traits often evolve independently in several different regions.

Molecular methods of inferring phylogeny are widely regarded to have both greater resolving power and accuracy than morphological techniques (Scotland et al. 2003; Wortley and Scotland 2006). The greater biogeographic congruence of molecular topologies analysed in this study provides further evidence that molecular topologies are generally more accurate than morphological counterparts. One of the most frequently cited advantages of molecular data (Hillis 1987; Donoghue and Sanderson 1992) is the vast amount of information available with which to infer relationships (often orders of magnitude more than available from morphology). Larger datasets are often expected to contain a greater number of informative characters, improving statistical power (Farris 2000), leading many authors to favour molecules *a priori*. Previous work comparing

congruence both within and between molecular and morphological samples found evidence that molecular trees were generally more consistent with each other than morphological trees. However, as congruence was high in most cases the authors warned against assuming molecular data was more reliable *a priori* (Pisani et al. 2007). Some measures of biogeographic congruence were found to improve slightly as the number of characters analysed to produce the tree increased, supporting the hypothesis that larger datasets improve phylogenetic accuracy, although the correlation was weak. As molecular datasets in the sample were significantly larger than morphological ones, it is likely that higher numbers of characters are at least partly responsible for the greater phylogenetic accuracy and, as a result, higher biogeographic congruence of molecular trees. The biogeographic patterns of extant taxa analysed in this study are likely to be most indicative of recent radiations of groups. It is plausible that molecular data is better able to resolve these recent diversifications, due to underlying sequences evolving more rapidly than phenotypic or morphological traits.

4.4.4 Biogeographic Patterns Of Convergence Are Present In Most Clades

The results of this study indicate that molecular trees are more reliable indicators of phylogeny than morphological trees in a significant number of cases. Convergent evolution of traits is one of, if not the, most common phenomenon responsible for phylogenetic error in morphological analyses. The pervasiveness of convergence has only been revealed relatively recently, with molecular analyses in a range of groups (Brower 1994; Lee 1998; Ruber and Adams 2001; Kearney and Stuart 2004) repeatedly supporting phylogenetic patterns which were not supported by morphology. These results suggest convergent evolution significantly impacts phylogenetic inference by contributing to high levels of homoplasy in morphological data (Wake et al. 2011; Ghiselin 2016). In morphological studies, character matrices are generally smaller and methods of inference traditionally used (parsimony) seek to maximise the fit of as many characters as possible (Kitching et al. 1998). It is, therefore, more likely that a greater proportion of the total number of characters will show homoplasy, making it easier for a few correlated convergent characters to dominate the phylogenetic signal. Homoplastic characters are, therefore, likely to be a particular problem in cladistic analyses of morphology, although there is evidence that lessening the influence of highly homoplastic characters through character weighting improves cladistic estimates in at least some cases (Goloboff and Carpenter 2008).

What exactly causes convergence to manifest in biogeographic patterns and the extent to which convergence can be attributed to adaptive or non-adaptive mechanisms is still very much under debate (Losos and Miles 2002; Losos 2011a). Many explanations of convergent evolution have focused on the importance of adaptation to new environments

and ecologies (Ruber and Adams 2001; Christin et al. 2007; Elmer and Meyer 2011). In the case of many island radiations, a limited number of ecological niches have been exploited multiple times independently on separate islands, correspondingly giving rise to the independent evolution of the same suites of morphological traits (Losos 1992; Pinto et al. 2008; Mahler et al. 2013). Non-adaptive mechanisms have been proposed, however, either as the result of genetic drift under neutral evolutionary models (Stayton 2008) or as the result of strong biological constraints (Wroe and Milne 2007; Losos 2011a). Identifying the causes of convergence, therefore, requires tests of the predictions these different hypotheses make. The adaptive theory of convergence predicts that in instances where taxa colonise new niches (for example due to expanding their range into new environments), diversification should be associated with the evolution of phenotypic traits. Even more importantly, subsequent events in which unrelated taxa colonise similar environments should produce a similar selection of phenotypic traits. Therefore, while the true pattern of relationships will mirror the historical biogeography of the clade, grouping taxa based on phenotypic similarity will likely lead to erroneously grouping distantly related taxa together. The significantly higher biogeographic congruence of molecular phylogenies is indirect evidence for the adaptive evolution of convergent traits and ecological constraint. As genetic or developmental constraints are inherited and, therefore, shared by related taxa, a theory of convergence based only on intrinsic constraints would predict a phylogenetic, rather than a biogeographic signal to convergence, essentially parallelism ‘writ large’.

4.4.5 Biogeography & Stratigraphy Are Complimentary Tests Of Phylogeny

Molecular data and specifically multi-gene DNA studies have become the norm for most phylogenetic analyses of extant taxa (Drummond et al. 2006; Hundsdoerfer et al. 2009; Vélez-Zuazo and Agnarsson 2011). The biogeographic congruence analyses in this chapter in most cases support the primacy of inferences based on molecular data over those based on morphology. This poses an important question: how do we attempt to accurately infer phylogeny in cases where sequence data is impossible to obtain? This concern is, perhaps, most prevalent for the inference of relationships in extinct clades (Wiens 2004). To compound the issue, knowledge of the morphology of extinct organisms is almost always incomplete or biased in a manner which is likely to result in poorly resolved or erroneous phylogenies (Sansom 2015; Mounce et al. 2016; Sansom et al. 2016), although the effect this has been hotly debated (Wiens and Morrill 2011). Palaeontologists have often sought to use additional sources of information which are thought to be largely independent from the character data used to build evolutionary trees as a means of testing competing phylogenetic hypotheses, most commonly stratigraphy.

Tests of stratigraphic congruence (Huelsenbeck 1994; Wills et al. 2008; O'Connor and Wills 2016) are most powerful when the clade in question has sufficient dated fossil material to fit onto a topology. The greater the number of taxa with accurately dated fossil records in the clade, the more powerful the test of stratigraphic congruence. In this study, analyses of the small sample of clades failed to recover a significant difference in stratigraphic congruence between morphological and molecular trees. Overall stratigraphic congruence values were high (well above 0.5 in nearly all cases), in agreement with the findings of other authors (Benton and Hitchin 1997). This is probably due, primarily, to the clades being largely composed of extant taxa, as relatively few fossils can be assigned to extant taxa of low taxonomic rank (e.g. genera, species) and fossil first occurrences will tend to be clustered towards the recent (the clade's evolutionary history is truncated. Previous work supports this conclusion, as top-heavy clades (i.e. those that contain most of their diversity at or close to the present) are known to show higher stratigraphic congruence than bottom-heavy clades (O'Connor and Wills 2016). In many cases there was probably insufficient fossil data for many clades to robustly test difference in fit between competing phylogenies which may only differ in the positions of one or two terminal taxa, with more range overlap and fewer dated ranges a greater range of tree topologies will have identical fit.

Gap Excess Ratio (GER) metrics generally yielded higher fit values than other metrics, especially the modified GER (GER*), although the result was still non-significant for the small sample size analysed. Nearly all the clades analysed were vertebrates and most of those were mammalian. A prior study on a larger sample of mammalian phylogenies (Benton 1998) did demonstrate a significant difference in the stratigraphic fit of morphological and molecular phylogenies, although GER metrics were not tested. Older measures of congruence based on node consistency (SRC,SCI) were found to be higher for morphological trees, while a ghost range measure (only RCI was tested in the study) was found to be better for molecular trees. Some of these differences in support could be accounted for by morphological data providing more accurate estimates of phylogeny (at least at the time), although ghost range measures are likely better measures of fit with the stratigraphic record in most cases (Siddall 1997; Wills 1999; Wills et al. 2008). Fit of the GER*, thought to be the least biased measure of stratigraphic fit (O'Connor and Wills 2016), had not been compared between morphological and molecular trees prior to this study. As tests of biogeographic congruence on the same sample also fail to detect a significant difference in most cases, further analyses with a larger sample are needed specifically to assess the performance of various stratigraphic and biogeographic congruence measures relative to each other. As Biogeographic HER was the only metric to significantly favour molecular trees in this small sample, biogeographic congruence seems to be at least equivalent to stratigraphy in its support for different phylogenetic

hypotheses. Both approaches are, to a large degree, complimentary and likely useful in testing phylogenetic reconstructions and identifying homoplasy in different scenarios.

4.4.6 Conclusions

In order to examine the congruence of distributional data with phylogeny a new metric. The Biogeographic HER, was formulated. Biogeographic HER is likely the least biased measure of biogeographic congruence as it calculates fit relative to the expected random fit on that specific topology. However, regardless of the measure used, biogeographic congruence was found to be significantly higher for molecular phylogenies of extant clades that for morphological phylogenies of those same clades. Biogeographic distributions of taxa on trees are non-random for most clades, with taxa from the same regions clustering more on the tree than expected by chance. Together these two findings promote the use of biogeographic data in independently assessing different phylogenies, at least in extant taxa for which occurrence data is available. Furthermore, the assertion that molecular trees are likely to be more accurate indicators of evolutionary relationships is supported by biogeographic data. Such patterns are consistent with homoplasy frequently arising in morphological phylogenies due to the parallel convergent evolution of traits in different regions as groups diversify, suggesting ecological constraints may influence evolutionary trajectories.

Previous independent tests of phylogenetic hypotheses have largely focused on temporal patterns and, in particular, congruence with stratigraphy. While previous work has shown stratigraphic shows greater support for morphological trees, no evidence of this pattern was found in the small subsample of clades with suitable fossil records. This is likely to be a consequence of the limitation of the small sample size used in this study, as tests of biogeographic congruence also failed to recover a significant result (with the exception of Biogeographic HER). While more work is needed to compare the relative fit of stratigraphic and biogeographic measures with phylogeny, these results suggest using both approaches to complement each other may be the most fruitful methodology. For older clades with relatively complete fossil records stratigraphic data may well provide the best means of independently testing phylogenies. For more recent clades with poor fossil records, biogeographic data is likely to prove the more useful test of phylogenetic support.

5 Do Genome Duplications Facilitate Diversification?

5.1. Introduction

5.1.1 Chapter Summary

The findings of the previous chapters have illuminated a number of macroevolutionary patterns which are likely to be, at least in part, manifestations of convergent evolution. The majority of plant and animal clades show restricted disparity through much of their evolutionary history and frequently re-evolve the same character states. Geographically consistent convergent radiations appear to be relatively common and can often negatively impact morphological phylogenetic analyses. Taken together, these observations suggest that evolution may be more strongly constrained than previously realised. This chapter examines one expected consequence of strong genetic constraints: that whole genome duplications (or polyploidy) improve an organism's ability to evolve and speciate. It is found that polyploid clades contain significantly more species than non-polyploid sister clades, regardless of taxonomic affinity or rank. The diversity of many groups does indeed appear to be limited by genetic constraint, possibly accounting, in part, for the widespread prevalence of convergence across the tree of life.

5.1.2 Evolutionary Constraints

5.1.2.1 Extrinsic Constraints

Evolutionary constraints are usually classified as either intrinsic genetic or developmental factors on one hand, or as extrinsic environmental factors on the other (Wagner 1995; Wagner and Erwin 2006). Evolutionary biologists have for a long time pointed to phenotypic similarity in distantly related groups in similar environments as evidence for natural selection producing similar evolutionary adaptations (Simpson 1953; Harvey and Pagel 1991; Conway Morris 2004). Specific examples of convergence that have been influential in this regard include morphological similarities in Asian and North American groups of desert rodents (Mares 1993), streamlined bodyforms in sharks, tuna, ichthyosaurs and dolphins (Bernal et al. 2001; Lingham-Soliar and Plodowski 2007), succulent plants in the Euphorbiaceae and Cactaceae (Alvarado-Cárdenas et al. 2013) and similarities between New World and Old World nectar feeding birds (Fleischer et al. 2008). Convergent traits are often hypothesised to result from selective pressures either in environments where high levels of competition or specific physical requirements

strongly delimit a limited number of ‘adaptive peaks’ in the evolutionary landscape (Mahler et al. 2013). The development of phylogenetic comparative techniques has led to further quantitative tests linking convergently evolved traits to specific environments in clades (Ruber and Adams 2001; Elmer and Meyer 2011; Lindgren et al. 2012).

5.1.2.2 Intrinsic Constraints

Although many of the explanations for convergence have focused on adaptation and selective pressures, other explanations exist. Indeed, some workers have argued that no special mechanisms are necessarily required to explain convergence, as expected rates of convergence can be relatively high simply due to genetic drift under Brownian motion models (Stayton 2008). Furthermore, it has been suggested that the developmental trajectories of organisms tend to become more complex with time and with evolutionary distance from the root of the Tree of Life (Haeckel 1866). Groups certainly differ in their degree of morphological and developmental conservatism, hence, vertebrates have a longer and more complex embryology than annelid worms, and worms in turn than jellyfishes. In such cases it is often difficult to determine which features are conserved from a common ancestor and which are independently derived from later developmental changes, particularly when a taxon can be separated from its closest living relative by hundreds of millions of years of evolution. Complexity might tend to increase not only as developmental stages are appended to those of ancestors (Haeckel 1874; Olsson et al. 2017), but also because genes and parts of organisms at all levels acquire a greater number of functions and networks of functions (Carroll 2008). Pleiotropy is the process by which the acquisition of multiple functions makes it difficult to modify a gene, organ or pathway for one purpose without deleteriously affecting its role in some other process (Williams 1957). This predicts that the evolutionary flexibility of organisms might become reduced with evolutionary time, and that bodyplans might become ‘locked down’ or canalised (Hornstein and Shomron 2006; Peterson et al. 2009). If taxa share the same developmental or genetic framework and certain changes are less likely to have deleterious consequences than others, the variation on which selection acts will be biased towards these variables. For example, although a reduction in the number of cells in the limb buds of bolitoglossine salamanders has led to the repeated evolution of a reduced digit number, evidence suggests the loss was only adaptive in one case (Jaekel and Wake 2007). Similar mechanisms have been proposed to operate at the more fundamental genetic level, constraining genetic change along ‘lines of least resistance’ (Schluter 1996). Organisms sharing the same genetic architecture seem prone to independently evolving the same phenotypic traits via similar shifts in developmental or genetic pathways, a phenomenon often termed parallel evolution (Reznick et al. 1996; Sucena et al. 2003; Yoon and Baum 2004).

5.1.3 Genome Duplication, Polyploidy & The Removal Of Evolutionary Constraint

One of the predictions of hypotheses that invoke intrinsic constraints to explain convergent evolution is that evolutionary potential should be greater in circumstances where pleiotropic effects are removed. The most obvious situation in which this could arise is when genes are duplicated, giving rise to multiple identical functional copies. More rarely, the entire genome of a lineage is doubled or otherwise multiplied giving rise to 3 (triploid), 4 (tetraploid), 6 (hexaploidy) or more sets of chromosomes. This phenomenon is known as polyploidy or Whole Genome Duplication (WGD), to distinguish it from the much more common Small-scale Gene Duplication (SGD) of individual genes.

5.1.3.1 Genome Duplication

In some groups of organisms, duplication of the whole genome can give rise to polyploids (i.e. organisms with more than two complete sets of chromosomes). Both polyploidy and whole genome duplication are often used more or less interchangeably, although the former term is normally used to describe lineages which currently have more than two sets of chromosomes (Bennett 2004), while whole genome duplication refers to the historical event the lineage underwent to become polyploid (Ohno 1970). In particular, Whole Genome Duplications (WGDs) are typically used to refer to ancient ploidy events or palaeopolyploidy whereby genome duplications took place close to or at the root of major clades (Wolfe and Shields 1997; Van De Peer et al. 2009). WGDs are often proposed to have taken place in numerous angiosperm clades (Soltis and Soltis 2016) as well as at least twice in vertebrates (Dehal and Boore 2005), even though millions of years of subsequent genetic evolution has turned most of the resulting paralogues into novel genes. Therefore, taxa sufficiently derived from a WGD can be functionally diploid but ancestrally polyploid. Some workers use the term cryptopolyploidy (Sparrow and Nauman 1976) to distinguish these more ambiguous cases from clearly identifiable recently evolved polyploids (neopolyploids).

5.1.3.2 Types of Polyploidy

Classification of polyploidy is debated (Stebbins 1945; Tate et al. 2005), but is generally divided into two main types based on the process by which it arose (Stebbins 1950). Allopolyploidization occurs when two copies of the genome from two parent species hybridize to eventually give rise to a polyploid descendent containing chromosomes from both parent species. Allopolyploidization often occurs as a result of somatic chromosome doubling in a diploid hybrid, followed by selfing to produce tetraploids (Ramsey and Schemske 2002). Allopolyploids can also arise after errors in meiosis create unreduced

gametes which fuse to make a tetraploid, or through the 'triploid bridge' mechanism as a normal haploid gamete fuses with an unreduced diploid gamete (Husband 2004). Polyploids with uneven numbers of chromosome sets often produce sterile aneuploids (offspring with unequal chromosome complements) (Sandfaer 1973). However, fertile polyploids can still be produced from subsequent fusion of an unreduced triploid gamete and a normal haploid one to create a tetraploid hybrid (Husband 2000). Allopolyploid speciation seems to be especially common in plants and has been well-studied in several commercially important crops such as cotton (Wendel et al. 1995) and wheat (Matsuoka 2011). Animal allopolyploids also exist however, although known examples are much rarer (Dowling and Secor 1997). To date the best examples of animal allopolyploids are known in fish (Qin et al. 2010), anurans (Christiansen and Reyer 2009) and insects (Astaurov 1969; Tinti and Scali 1996).

Autopolyploidization is polyploidy without hybridization via the duplication of an organism's own homologous chromosomes. As autopolyploids have more than two sets of homologous chromosomes meiosis often results in multivalent chromosomes, a phenomenon known as polysomal inheritance. Polysomal inheritance, often taken to be diagnostic of autopolyploidy, has been identified in a number of polyploid plants (Stift et al. 2008; Landergott 2009). While multiple ploidy levels within species were recognised as common autopolyploid speciation was thought to be relatively rare (Stebbins 1950; Grant 1981), because it was thought that new polyploids would always have to out-compete conspecifics or establish themselves in new niches to survive. More recent studies show that autopolyploidy is more common in plants than previously realised, especially when the polyploid descents are geographically isolated from their diploid ancestors (Soltis et al. 2007). Autopolyploids are thought to account for around half of all polyploid species (Barker, Arrigo, et al. 2016), although these are only rough estimates due to issues such as limited sampling and difficulties in applying genetic definitions to taxonomic frameworks (Doyle and Sherman-Broyles 2017).

All forms of polyploidy are cell-specific and while polyploidy is commonly used to refer to cases where all non-gametic cells are polyploid, cell-type or tissue-specific forms of polyploidy also exist. This phenomenon is known as endopolyploidy. Examples include, but are no means limited to, the endosperm of many flowering plants (D'Amato 1964), the secretory cells of ants and bees (Scholes et al. 2014; Rangel et al. 2015) and mammalian trophoblast cells (Anatskaya and Vinogradov 2004). Endopolyploidy is theorised to have several important effects, namely being linked to increased cell size, rapid growth and early maturation (Neiman et al. 2017).

5.1.4 Known Examples of Polyploidy

5.1.4.1 Polyploidy in Plants

Polyploidy is thought to be extremely widespread in plants, with many species showing evidence of multiple successive rounds of gene duplication in their history (Adams and Wendel 2005). Neopolyploids seem to be particularly common in angiosperms (Ramsey and Schemske 1998) and ferns (Wagner and Wagner 1980). Although the frequency of polyploidy is debated (Soltis et al. 2004) recent authors have estimated that around 15% of angiosperm and 31% of fern speciation is linked to a ploidy increase (Wood et al. 2009), around 4 times higher than previous estimates (Otto and Whitton 2000). Examples of polyploidy are abundant in both the monocots (Goldblatt 1980; Paterson et al. 2012) and the eudicots (Lewis 1980). Within the monocots most members of the grass family (Poaceae) are highly polyploid (Levy 2002) and grasses such as sugarcane have been intensively studied as model polyploid genomes (Grivet et al. 1996; Raboin et al. 2008). In the eudicots, polyploidy is common such diverse and speciose clades as the Brassicaceae (Town et al. 2006), Fabaceae (Cannon et al. 2015), Violaceae (Marcussen et al. 2012) and Orchidaceae (Hedrén et al. 2007). Even the relatively small genome of *Aribadopsis* was likely significantly shaped by several ploidy events both recent and ancient (Blanc et al. 2003).

5.1.4.2 Polyploidy in Other Groups

Polyploidy in animals has traditionally thought to be relatively rare (Otto and Whitton 2000), but is being recognised in an increasing number of groups, particularly amphibians and fish (Mable et al. 2011). Polyploidy occurs in many groups of actinopterygians, especially teleosts (Braasch and Postlethwait 2012). Notable examples studied cases include salmonids (Allendorf et al. 2015), catfish (Garcia et al. 2003) and carp (David et al. 2003). Neopolyploidy also seems to be fairly common in amphibians (Beçak et al. 1970), particularly anurans (Haddad et al. 1994; Martino and Sinsch 2002). Polyploidy has also been studied to a lesser extent in other groups, such as insects (Morgan 1925; Lokki and Saura 1980), crustaceans (Salemaa 1984) and molluscs (Lee 1999). There are few known examples of polyploidy in fungi, although there are likely many cryptic polyploid species (Rogers 1973; Albertin and Marullo 2012). Polyploid organisms often seem to show different distributions than their diploid relatives, favouring more extreme environments (Love and Love 1943). Polyploids in many groups seem to be concentrated at high latitudes compared to diploid relatives (Johnson and Packer 1965), although this may not only be environmental. It has been hypothesised that many polyploidisation events occurred post-glacially as species from previous isolated habitats hybridised (Kearney 2005).

5.1.4.3 Palaeopolyploidy

Ancient examples of Whole Genome Duplications or palaeopolyploidy are rarer and more difficult to confirm but are thought to have played an important role in the origins of several major clades (Kenny et al. 2016; Tiley et al. 2016). Research suggests that a WGD occurred early on in the evolution of yeast (Wolfe and Shields 1997; Kellis et al. 2004). Most major clades of angiosperms are also thought to have originated through polyploidy (Soltis and Soltis 2016), notably in the grasses, crucifers and legumes in addition to major clades such as monocots and rosids. Similar duplication events may have also occurred basally other seed plants (Li et al. 2015). In animals, hypotheses of Whole Genome Duplication are more controversial. Perhaps the best-known example of WGDs putatively facilitating morphological novelty occurs early in the history of vertebrates, where two WGD events have been linked to the evolution of the vertebrate bodyplan and the subsequent diversification of the gnathostomes respectively (Dehal and Boore 2005). However, the recent inclusion of extinct stem groups with 'mosaic' bodyplans has cast doubts on this interpretation. It seems likely that the assembly of vertebrate and gnathostome bodyplans happened more gradually, rather than as part of a rapid burst of evolution, introducing considerable uncertainty as to when the WGD actually took place (Donoghue and Purnell 2005).

5.1.5 Possible Consequences Of Polyploidy

5.1.5.1 Physiological Effects

Polyploidy is associated with a number of significant physiological effects at both the cell and organism level (Comai 2005). Polyploidy is often associated with an increase in cell size and gene expression levels, which can have positive effects on the growth of tissues (Neiman et al. 2017), but also alter cell architecture and regulatory mechanisms (Jaekel and Wake 2007). While polyploidy appears to be directly linked to body size in nematodes (Flemming et al. 2000), in most cases developmental mechanisms appear to regulate growth to compensate and no effect on body size is seen (Fankhauser 1945; Henery et al. 1992). The positive effects of increased gene expression and interaction in polyploid hybrids is normally grouped under the broad category 'heterosis' or 'hybrid vigour' effects (Akanno et al. 2018). In reality, polyploidy affects gene expression in complex ways. Studies in maize have shown that while the polyploidy can cause increases in the expression of many genes, downregulation of genes also occurs (Guo et al. 1996).

5.1.5.2 Effects On Reproduction

One major disadvantage of polyploidy is that it can introduce errors into both meiosis and mitosis, producing aneuploid cells which, it has been suggested, are more

susceptible to cancers (Matzke et al. 2003). These errors can result in polyploid organisms being sterile (Standish et al. 1978) or in extreme cases having severe developmental defects that drastically decrease life expectancy (Fechheimer 1981). One of the reasons polyploidy is thought to be more common in plants is that the genetic and developmental architecture of plants is far more resilient to these kinds of negative side effects (Leitch and Leitch 2008). Sterility in polyploids is often countered by a greatly increased capacity for selfing due to a higher chromosome compliment (Miller and Venable 2000), meaning many polyploids reproduce asexually via parthenogenesis (Bierzychudek, Lewis 1985). Allopolyploidy and autopolyploidy creating infertile yet selfing hybrids is regarded as one of, if not the, single most important mechanism by which reproductive isolation (and hence speciation) can instantaneously occur (Soltis and Soltis 2009).

5.1.5.3 Evolution Of Novel Genes

One of the most important evolutionary consequences of polyploidy is that it greatly increases the number of redundant genes as the organism gains new copies of all its genes. Because these new copies are initially identical, they can be freed from the pressure to maintain their old functions. These duplicate genes often appear to be subject to relaxed selection pressures and may persist in the genome for long periods of time (Aagaard et al. 2006). This may allow one copy to mutate and evolve novel functions, ‘under the radar’ of normal selective pressure, and thereby crossing adaptive valleys (Zhang et al. 1998). Polyploidy is therefore thought to be the most important originator of novel genes (Zhang 2003), greatly contributing to the expansion of gene families (Hamel et al. 2006). This process seems to have been particularly important in giving rise to regulatory gene networks. Arthropods and flowering plants are both groups prone to genome duplication, with body plans controlled by homeotic genes (Weigel and Meyerowitz 1994; Hughes and Kaufman 2002). In these groups, important traits such as flowers (Weigel and Meyerowitz 1994) and limbs (Averof and Akam 1995) share common segmented templates. Gene duplication through polyploidy, followed by subsequent modification has been proposed as an easy means of evolving more complex regulatory networks in some groups, allowing for greater partitioning and autonomy of gene expression (Averof et al. 1996).

5.1.6 Aims

While it has been proposed that macroevolutionary patterns, specifically the prevalence of convergent evolution, may the result of genetic constraints, empirical evidence for the widespread impact of such constraints through the history of life is lacking. This chapter aims to investigate one of the most important and easily testable predictions of the constraint hypothesis, namely that polyploidy relaxes genetic constraints and, therefore, facilitates genotypic and phenotypic diversification. More specifically, it seeks to identify whether there is a significant difference in the number of species found in clades associated with polyploidy events relative to sister clades lacking such events.

The study in this chapter testing for a difference in the diversity of polyploid and non-polyploid clades has the following aims:

i) To thoroughly search the biological literature to identify and compile published occurrences of polyploidy from as diverse a range of plant and animal clades as possible.
ii) To use current phylogenetic knowledge of clade relationships to identify the most closely related clade lacking the ploidy event, for each polyploid clade.
iii) To estimate the number of polyploid and non-polyploid species in each clade being compared using online repositories and taking into account the known fossil record of groups.
iv) To test whether there are significantly more species in polyploid clades relative to non-polyploid sister clades.

5.2. Methods

The aim of this study's methodology was to test the following hypothesis:

H_1: Clades containing an increase in ploidy level have a greater number of species than sister clades which do not show an increase in ploidy level.

H_0: Clades containing an increase in ploidy level do not have a greater number of species than sister clades which do not show an increase in ploidy level.

5.2.1 Sample Collection & Identifying Ploidy Increases

Biological publications spanning the years 1950 to 2016 were searched for known cases of polyploid taxa (Appendix 3). Sampling effort was focused on obtaining a significant sample size of polyploid clades for as wide a range of groups as possible, over accurately representing the proportion of polyploid taxa in different groups. As a result, the literature of clades for which polyploids were rarely documented (e.g. annelids) was more intensively sampled than that of clades for which polyploidy was extremely common (e.g. flowering plants). Instances of somatic polyploidy (endopolyploidy) and non-naturally occurring polyploids were discounted, due to these cases representing phenomena other than those which were thought to directly relate to diversification and speciation.

Polyploidy was only identified at the genus level and higher. Although comparing specific clades of species and subspecies within genera would be desirable to more accurately reflect all polyploidy events, phylogenies at this level are often poorly supported with high proportions of missing taxa. This makes identifying sister clades confidently impossible in many cases, even when the relationships of taxa are resolved, as such relationships are very likely to change in the near future. Although groups of higher rank were included, such as families and orders, most instances of polyploidy occur at the genus level or below and so it was seen as important to ensure these smaller scale events were included in the analysis. Extinct taxa were also included in diversity estimates wherever possible, with comparisons between genera in most cases being the lowest rank at which it is reasonable to utilize fossil data.

In most cases, polyploid clades were simply taken directly from the publication. If polyploidy was identified at the species level, those species were compared to close relatives to determine whether polyploidy was unique to that species or shared by other taxa in the same genus. If polyploidy was found to occur in other species within the genus then the genus was classed as polyploid, otherwise the genus was not included as a polyploid clade. In cases where species showed both diploid and polyploid subspecies or species morphs, the entire species was classed as polyploid. Some groups,

particularly many angiosperm clades, contained multiple nested ploidy levels (e.g. hexaploids nested within a clade of tetraploids). Nested ploidy events that could be localised to a monophyletic clade at the taxonomic rank of genus or higher were treated separately, otherwise polyploids of different levels were treated as a single polyploid clade. Although this method allows polyploid clades to be rapidly identified and delineated from the existing literature, it has the disadvantage of classifying multiple independent ploidy events as a single polyploid clade in the dataset. Some of the polyploid clades identified were themselves nested within larger polyploid or non-polyploid clades. As there is no bias in whether polyploid clades are nested within clades characterised as non-polyploid or vice versa, these phenomena are unlikely to bias diversity estimates to favour one clade type over the other.

5.2.2 Identifying Non-polyploid Sister Clades

Phylogenetic studies from the years 1975 to 2017 were used to identify sister clades to polyploids. In cases where multiple phylogenies were found, the most recently published one was used. The only exceptions to this were cases where polyploid clades were part of a polytomy, in which case older phylogenies which resolved the polytomy were used if available. Cases where it was impossible to resolve a polytomy containing the polyploid clade and other non-polyploid clades were discounted. In cases where the sister group of a polyploid clade was also found to be polyploid, the least inclusive clade containing both polyploidy groups was defined as the new polyploid clade and its sister clade used as the non-polyploid clade. All clade pairs, therefore, consisted of one polyploid clade which was inferred to contain an increase in ploidy level and one non-polyploid clade that was inferred to not contain an increase in ploidy level. As clades were evaluated as comparable if they were phylogenetic sister clades, groups of different taxonomic ranks could be compared, although as taxonomy generally agreed with phylogeny, this was rare. More commonly, multiple taxonomic groups were contained within one or more of the clades being compared (e.g. several genera being compared to one genus) although as both clades originate from the same node in the tree (i.e. of the same phylogenetic level) these comparisons were perfectly valid.

5.2.3 Estimating Number Of Species In Clades

The number of species in each clade was estimated using online biodiversity databases. For vertebrates, FishBase (Froese and Pauly 2017) was used for various fish groups, AmphibiaWeb (Anon 2018) for lissamphibian taxa, The Reptile Database (Uetz et al. 2017) for reptile groups, Avibase (Lepage et al. 2014) for birds and Mammal Species of

the World (Woods and Kilpatrick 2005) for mammals. For invertebrates, the Catalogue of Life Integrated Taxonomic Information System (Roskov et al. 2018), BioLib (Zicha 2018), and Systema Dipterorum (Pape and Thompson 2013) were used for insects, the World Register of Marine Species (WoRMS Editorial Board 2018) and the Catalogue of Life Integrated Taxonomic Information System for annelids, nematodes and crustaceans and the Worldwide Mollusc Species Database (Galli 2016) used for molluscs . All plant diversity estimates were taken from The Plant List (The Plant List 2017). For a small minority of clades diversity estimates also had to be made from the original source publications. Only species names known to be valid were counted, synonymies or species names that had not been reviewed were not included. The fossil record of each clade was also checked using the Fossilworks portal of the Paleobiology Database (Alroy 2013) and Google Scholar searches including the keywords of the clade name and 'fossil', to ensure that as many extinct representatives as possible were included.

5.2.4 Statistical Analyses

In order to determine whether the number of species in polyploid clades was significantly greater than in non-polyploid clades, paired Wilcoxon signed-rank tests were performed on the species counts in both the polyploid and non-polyploid clade groups. Wilcoxon tests were chosen as species counts of the majority of groups were found to be non-normally distributed (their distributions had long tails). Paired tests were carried out due to the non-independence of each pair of data being sister clades and therefore expected to show phylogenetic correlation. Separate statistical tests were performed on the whole dataset as increasingly finely divided taxonomic subdivisions representing major clades and grades of organism, as limited by available sample size.

As the nesting of polyploid clades introduces an element of non-independence into data being statistically compared, separate analyses were performed on only genera in the dataset. As the clades in this subset were all of the same taxonomic rank, there was no nesting and therefore each pair of clades could essentially be taken as an independent test of the hypothesis, at the cost of a slightly reduced sample size. Effects of polyploidy on diversity could be scale dependent, in which any patterns recovered could be biased by the sample of clades in the dataset. In order to determine whether taxonomic rank had an effect on differences in diversity between polyploid and non-polyploid clades, paired Wilcoxon signed-rank tests were also carried out on the sample of clades of higher taxonomic rank, as well as individual taxonomic ranks with sufficient sample size.

5.3 Results

5.3.1 Taxonomic Affinity & Diversity Of Polyploid & Non-Polyploid Clades

A systematic review of the literature was made in order to identify pairs of 'polyploid' and 'non-polyploid' sister groups. This yielded data for 712 clades, comprising 356 pairs of 'polyploid' and 'non-polyploid' clades (**Table 5.1**). The number of species in a non-polyploid clade ranged from a minimum of 1 to a maximum of 3,286, with a mean of 93 and a median of 15. The number of species in polyploid clades ranged even from 1 to 82,320, with a mean of 406 and a median of 52. The maximum value of 82,320 species is in fact an outlier belonging to the 'true' weevils (Curculionidae), one of the largest of all animal families. Removing this clade lowered the maximum number of species in polyploid clades to 4,719, with a mean of 175 species: still markedly higher than that of non-polyploid clades. Although a conscious effort was made to sample as evenly as possible throughout the animal and plant kingdoms, the sample is uneven, largely because there are far fewer recorded instances of polyploidy in some groups than others. Whilst the dataset contained similar numbers of animal and plant clades (153 animal and 203 plant clade pairs) subsets varied greatly in size. Within animals, there were more documented cases of polyploidy within vertebrates (91 clade pairs) than invertebrates (62 pairs), while within plants there were far more cases of polyploidy found within angiosperms (128 clade pairs) than in all other plant groups (non-angiosperms: 75 clade pairs). Most instances of polyploidy in vertebrates were within groups of fishes (42 clade pairs) with the modern lissamphibians (Lissamphibia, 29 clade pairs) as the next largest subset. In the invertebrates most polyploid clades were insects (32 clade pairs), with polyploidy either rare or poorly documented in other groups. Examples of polyploidy in angiosperms were largely within the eudicots (91 clade pairs vs. 27 in monocots) with ferns constituting the next largest sample in plants (69 clade pairs). A few animal groups had sample sizes small enough that they had to be omitted from separate analysis, namely birds (2 clade pairs, in Phasianinae and Arini) and mammals (1 clade pair, in Octodontidae) within the vertebrates, and nematodes (1 clade pair, in Ascarididae) within invertebrates. A number of the clades also had sample sizes much smaller than the other groups but large enough to include in the analysis, including reptiles (17 clade pairs), annelid worms (13 clade pairs), molluscs (10 clade pairs), crustaceans (6 clade pairs), the clade containing magnolids and chloranthales near the base of angiosperms (9 clade pairs) and gymnosperms (6 clade pairs).

Group	Subgroup	Taxonomic Level	Parent Clade	Non-Polyploid Clade	Number of Species	Polyploid Clade	Number of Species
Vertebrate	Fish	Order	Basal Ray-fins	Lepisosteiformes	33	Acipenseriformes	55
Vertebrate	Fish	Order	Protacanthopterygii	Esociformes	20	Salmoniformes	231
Vertebrate	Fish	Suborder	Trachichthyiformes	Trachichthyoidea	62	Diretmidae	5
Vertebrate	Fish	Family	Cyprinodontiformes	Anablepidae	18	Poeciliidae	349
Vertebrate	Fish	Family	Perciformes	Anabantidae	33	Channidae	39
Vertebrate	Fish	Family	Cypriniformes 1	Gyrinocheilidae + Vaillantellidae	6	Catostomidae	79
Vertebrate	Fish	Family	Cypriniformes 2	Nemacheilidae	630	Cobitidae	261
Vertebrate	Fish	Family	Cypriniformes 3	Vaillantellidae	3	Balitoridae + Cobitidae + Nemacheilidae	990
Vertebrate	Fish	Family	Characiformes	Prochilodontidae	21	Curimatidae	105
Vertebrate	Fish	Family	Siluriformes 1	Asteroblepidae	54	Loricariidae	719
Vertebrate	Fish	Family	Siluriformes 2	Amblycipitidae + Sisoridae	196	Bagridae	255
Vertebrate	Fish	Family	Siluriformes 3	Pimelodidae	97	Siluridae	109
Vertebrate	Fish	Family	Siluriformes 5	Anchariidae	6	Ariidae	166
Vertebrate	Fish	Family	Siluriformes 6	Scoloplacidae + Asteroblepidae	60	Callichthyidae	206
Vertebrate	Fish	Family	Petromyzontiformes	Geotriidae + Mordaciidae	4	Petromyzontidae	42
Vertebrate	Fish	Subfamily	Cyprinidae 1	Tincinae	10	Leuciscinae	575
Vertebrate	Fish	Tribe	Cyprinidae 2	Spinibarbini	7	Schizothoracini	100
Vertebrate	Fish	Genus	Lepidosireniformes	Lepidosiren	2	Protopterus	8
Vertebrate	Fish	Genus	Scaphirhynchinae	Pseudoscaphirhynchus	4	Scaphirhynchus	4
Vertebrate	Fish	Genus	Gobioninae	Romanogobio	21	Gobio	164
Vertebrate	Fish	Genus	Leuciscinae	Lavnia	42	Ptychocheilus	11
Vertebrate	Fish	Genus	Cyprininae 1	Cyprinion	9	Barbus sensu sricto & Aulopyge	34
Vertebrate	Fish	Genus	Cyprininae 2	Neolissochilus	28	Labeobarbus	126
Vertebrate	Fish	Genus	Cyprininae 3	Petroleuciscus	7	Squalius	104
Vertebrate	Fish	Genus	Cyprininae 4	Luciobarbus	47	Capoeta	77
Vertebrate	Fish	Genus	Clariidae	Bathyclarias	13	Clarias	180
Vertebrate	Fish	Genus	Callichthyinae	Dianema	17	Hoplosternum	22
Vertebrate	Fish	Genus	Callichthyidae	Aspidoras	22	Corydoras	216
Vertebrate	Fish	Genus	Channidae	Parachanna	3	Channa	61
Vertebrate	Fish	Genus	Barbinae	Enteromius	210	Pseudobarbus	15
Vertebrate	Fish	Genus	Torpedinidae	Tetronarce	12	Torpedo	11
Vertebrate	Fish	Genus	Squaliformes 1	Cephaloscyllium	18	Scyliorhinus	52
Vertebrate	Fish	Genus	Squaliformes 2	Scymnodon	4	Oxynotus	5
Vertebrate	Fish	Genus	Siluriformes 4	Clariidae	118	Heteropneustus	5
Vertebrate	Fish	Genus	Ginglymostomatidae	Pseudoginglymostoma	1	Ginglymostoma	23
Vertebrate	Fish	Genus	Oxynotidae	Centroscymnus	12	Oxynotus	5
Vertebrate	Fish	Genus	Scyliorhinidae	Poroderma	6	Scyliorhinus	72
Vertebrate	Fish	Genus	Polyodontidae	Psephurus	1	Polyodon	2
Vertebrate	Fish	Genus	Botiidae	Chromobotia + Yasuhikotakia + Ambastaia	12	Botia	67
Vertebrate	Fish	Genus	Cobitidae	Sabanejewia	16	Cobitis	244
Vertebrate	Fish	Genus	Sternopygidae	Distocyclus	3	Eigenmannia	15
Vertebrate	Fish	Genus	Gymnotidae	Electrophorus	1	Gymnotus	52
Vertebrate	Fish	Genus	Cyprinidae 3	Spinibarbini	7	Schizothorax	100

Table 5.1 Clades used in the analysis of the diversity of polyploid clades. Includes: The largest clade within animals or plants to which the parent clade belongs (Group), Smallest phylogenetic grouping of parent clades analysed in the study (Subgroup), The taxonomic rank of the parent clade (Taxonomic Level), The smallest clade containing both the polyploid and non-polyploid clades (Parent Clade), clades not containing an increase in ploidy level (Non-Polyploid Clade) and clades which contain at least one increase in ploidy level (Polyploid Clade).

Group	Subgroup	Taxonomic Level	Parent Clade	Non-Polyploid Clade	Number of Species	Polyploid Clade	Number of Species
Vertebrate	Lissamphibian	Family	Urodela	Salamandroidea + Cryptobranchoidea	520	Sirenidae	16
Vertebrate	Lissamphibian	Genus	Astylosterninae	Trichobatrachus	1	Astylosternus	12
Vertebrate	Lissamphibian	Genus	Bufonidae 1	Dendrophryniscus	10	Bufo	161
Vertebrate	Lissamphibian	Genus	Bufonidae 2	Amietophrynus	38	Sclerophrys	45
Vertebrate	Lissamphibian	Genus	Bombinatoridae	Barbourula	2	Bombina	8
Vertebrate	Lissamphibian	Genus	Dicroglossidae	Euphlyctis	7	Hoplobatrachus	5
Vertebrate	Lissamphibian	Genus	Hylidae 1	Tlalocohyla + Isthmohyla + Triprion + Anotheca + Smilisca	30	Hyla + Dryophytes	37
Vertebrate	Lissamphibian	Genus	Hylidae 2	Phasmahyla	7	Phyllomedusa	30
Vertebrate	Lissamphibian	Genus	Craugastorinae	Craugastor	110	Haddadus	3
Vertebrate	Lissamphibian	Genus	Holoadeninae	Bryophryne	13	Holoaden	4
Vertebrate	Lissamphibian	Genus	Archaeobatrachia	Ascaphus	2	Leiopelma	7
Vertebrate	Lissamphibian	Genus	Eleutherodactylinae	Diasporus	15	Eleutherodactylus	192
Vertebrate	Lissamphibian	Genus	Alsodidae	Alsodes	19	Eupsophus	10
Vertebrate	Lissamphibian	Genus	Pyxicephalinae	Aubria	2	Pyxicephalus	4
Vertebrate	Lissamphibian	Genus	Ranidae 1	Odorrana	62	Rana	116
Vertebrate	Lissamphibian	Genus	Ranidae 2	Meristogenys	13	Pelophylax	26
Vertebrate	Lissamphibian	Genus	Leiuperidae	Physalaemus + Engystomops + Edalorhina	59	Pleurodema	15
Vertebrate	Lissamphibian	Genus	Ceratophryidae	Chacophrys + Lepidobatrachus	4	Ceratophrys	8
Vertebrate	Lissamphibian	Genus	Cycloramphibidae	Macrogenioglottus	1	Odontophrynus	11
Vertebrate	Lissamphibian	Genus	Microhylidae 1	Elachistocleis + Hamptophryne + Gastrophryne	23	Chiasmocleis	20
Vertebrate	Lissamphibian	Genus	Microhylidae 2	Barygenys	9	Cophixalus	61
Vertebrate	Lissamphibian	Genus	Microhylidae 3	Paradoxophyla	2	Scaphiophryne	9
Vertebrate	Lissamphibian	Genus	Pipidae 1	Silurana	2	Xenopus	22
Vertebrate	Lissamphibian	Genus	Pipidae 2	Hymenochirus	4	Silurana + Xenopus	24
Vertebrate	Lissamphibian	Genus	Lymnodynastidae	Notaden	4	Neobatrachus	10
Vertebrate	Lissamphibian	Genus	Pyxicephalidae	Strongylopus + Poyntonia + Microbatrachella + Cacosternum	29	Tomopterna	15
Vertebrate	Lissamphibian	Genus	Salamandroidea	Dicamptodon	6	Ambystoma	33
Vertebrate	Lissamphibian	Genus	Pleurodelinae 1	Calotriton	2	Triturus	11
Vertebrate	Lissamphibian	Genus	Pleurodelinae 2	Mesotriton	10	Lissotriton	10
Vertebrate	Reptile	Genus	Amphibolurinae	Lophognathus	5	Amphibolurus	7
Vertebrate	Reptile	Genus	Agamidae	Hydrosaurus +Amphibolurinae	121	Leiolepis	9
Vertebrate	Reptile	Genus	Gekkonidae 1	Hemiphyllodactylus	19	Gehyra	48
Vertebrate	Reptile	Genus	Gekkonidae 2	Cyrtodactylus	232	Hemidactylus	144
Vertebrate	Reptile	Genus	Gekkonidae 3	Dixonius	8	Heteronotia	5
Vertebrate	Reptile	Genus	Gekkonidae 4	Luperosaurus	13	Lepidodactylus	33
Vertebrate	Reptile	Genus	Iguanidae	Urosaurus	26	Sceloporus	101
Vertebrate	Reptile	Genus	Lacertinae	Timon	6	Lacerta	45
Vertebrate	Reptile	Genus	Teiidae 1	Ameiva	36	Cnemidophorus	59
Vertebrate	Reptile	Genus	Teiidae 2	Ameiva	7	Aspidoscelis	11

Table 5.1 Clades used in the analysis of the diversity of polyploid clades continued (1)

Group	Subgroup	Taxonomic Level	Parent Clade	Non-Polyploid Clade	Number of Species	Polyploid Clade	Number of Species
Vertebrate	Reptile	Genus	Typhlopidae	Anilios	46	Indotyphlops	24
Vertebrate	Reptile	Genus	Chelidae	Acanthochelys	4	Platemys	1
Vertebrate	Reptile	Genus	Viperidae	Crotalus + Sistrurus	47	Agkistrodon	6
Vertebrate	Reptile	Genus	Typhlopidae	Acutotyphlops	4	Ramphotyphlops	49
Vertebrate	Reptile	Genus	Gymnophthalmidae	Arthrosaura	2	Leposoma	6
Vertebrate	Reptile	Genus	Scincidae	Emoia	15	Menetia	6
Vertebrate	Reptile	Genus	Tropiduridae	Phymaturus	47	Liolaemus	256
Vertebrate	Bird	Genus	Phasianinae	Bambosicola	3	Gallus	14
Vertebrate	Bird	Genus	Arini	Primolius	3	Ara	10
Vertebrate	Mammal	Genus	Octodontidae	Otomys	28	Tympanoctomys	4
Invertebrate	Insect	Family	Curculionoidea	Brentidae	1758	Curculionidae	82320
Invertebrate	Insect	Subfamily	Chamaemyiidae	Leucopinae	183	Chamaemyiinae	165
Invertebrate	Insect	Genus	Ptininae	Sphaericus	1	Ptinus	42
Invertebrate	Insect	Genus	Eumolpinae	Colasposoma	5	Bromius	2
Invertebrate	Insect	Genus	Alticini	Aphthona	7	Altica	74
Invertebrate	Insect	Genus	Doryphorina	Zygogramma	13	Calligrapha	38
Invertebrate	Insect	Genus	Xyleborini	Theoborus + Coptoborus + Sampsonius + Dryocoetoides	100	Xyleborus	1524
Invertebrate	Insect	Genus	Ipini	Pityogenes	40	Orthotomicus + Ips	235
Invertebrate	Insect	Genus	Pityophthorina	Conophthorus	25	Pityophthorus	548
Invertebrate	Insect	Genus	Scolytinae	Hylesinopsis + Haplogenius + Strombophorus + Ctonoxylon + Hypothenemus + Hylesinus	650	Dendroctonus	47
Invertebrate	Insect	Genus	Chrysomelinae	Zygogramma	13	Calligrapha	37
Invertebrate	Insect	Genus	Archostemata	Crowsoniella	1	Micromalthus	4
Invertebrate	Insect	Genus	Blosyrini	Blosyrodes + Blosyrosoma + Bradybamon + Dactylotus + Holonychus + Proscephaladeres	73	Blosyrus	85
Invertebrate	Insect	Genus	Listroderini	Methypora + Rupanius + Acrorius + Trachoderma + Lamiarhinus + Philippius + Germainiellus	32	Listroderes	183
Invertebrate	Insect	Genus	Entiminae	Naupactus + Barynotus + Strophosoma + Liophloeus + Polydrusus	538	Otiorhynchus	1288
Invertebrate	Insect	Genus	Orthocladinae 1	Mesosmittia	16	Limnophyes	141
Invertebrate	Insect	Genus	Orthocladiinae 2	Ferringtonia	1	Pseudosmittia	93
Invertebrate	Insect	Genus	Tanytarsini	Tanytarsus	470	Paratanytarsus	69
Invertebrate	Insect	Genus	Agromyzidae	Napomyza	79	Phytomyza + Chromatomyia	703
Invertebrate	Insect	Genus	Psychodini	Psychomora	1	Psychoda	365
Invertebrate	Insect	Genus	Simuliini	Stegopterna	15	Cnephia	12

Table 5.1 Clades used in the analysis of the diversity of polyploid clades continued (2)

Group	Subgroup	Taxonomic Level	Parent Clade	Non-Polyploid Clade	Number of Species	Polyploid Clade	Number of Species
Invertebrate	Insect	Genus	Prosimuliini	Pedrowygomyia	4	Prosimulium	160
Invertebrate	Insect	Genus	Oligotomidae	Oligotoma	25	Haploembia	10
Invertebrate	Insect	Genus	Coccidae	Eulecanium	50	Physokermes	11
Invertebrate	Insect	Genus	Delphacidae	Nilaparvata	17	Muellerianella	7
Invertebrate	Insect	Genus	Diprionidae	Neoprion	14	Diprion	3
Invertebrate	Insect	Genus	Apidae	Scaura	5	Melipona	63
Invertebrate	Insect	Genus	Psychidae	Siederia	8	Dahlica	45
Invertebrate	Insect	Genus	Blaberidae 1	Epilampra	70	Pycnoscelus	15
Invertebrate	Insect	Genus	Blaberidae 2	Blaberus	6	Eublaberus	9
Invertebrate	Insect	Genus	Tettigoniidae	Clonia + Cloniella + Peringueyella	27	Saga	15
Invertebrate	Annelid	Family	Crassiclitellata 1	Hormogastridae	31	Lumbricidae	251
Invertebrate	Annelid	Family	Crassiclitellata 2	Acanthodrilidae	193	Megascolecidae	467
Invertebrate	Annelid	Subfamily	Naididae	Phallodrilinae + Rhyacodrilinae	750	Tubificinae	723
Invertebrate	Annelid	Genus	Tubificinae	Limnodrilus	70	Tubifex	91
Invertebrate	Annelid	Genus	Lumbricidae 1	Allolobophora	12	Dendrobaena	16
Invertebrate	Annelid	Genus	Lumbricidae 2	Postandrilus	6	Aporrectodea	46
Invertebrate	Annelid	Genus	Lumbricidae 3	Eiseniona	3	Eiseniella	6
Invertebrate	Annelid	Genus	Lumbricidae 4	Octodrilus	40	Octolasion	5
Invertebrate	Annelid	Genus	Lumbricidae 5	Eisenia + Eisenoides	32	Lumbriculus	4
Invertebrate	Annelid	Genus	Cirratulidae	Ctenodrilus	2	Dodecaceria	6
Invertebrate	Annelid	Genus	Megascolecidae 1	Begemius	6	Amynthas	488
Invertebrate	Annelid	Genus	Megascolecidae 2	Trigaster + Neotrigaster	33	Diplocardia	48
Invertebrate	Annelid	Genus	Enchytraeidae	Grania	87	Lumbricillus	113
Invertebrate	Nematode	Genus	Ascarididae	Ascaris	2	Parascaris	1
Invertebrate	Crustacean	Genus	Pontoporeiidae	Monoporeia + Diporeia	3	Pontoporeia	13
Invertebrate	Crustacean	Genus	Anostraca	Parartemia	2	Artemia	10
Invertebrate	Crustacean	Genus	Cambaridae	Troglocambarus	1	Procambarus	160
Invertebrate	Crustacean	Genus	Daphniidae	Simocephalus	30	Daphnia	38
Invertebrate	Crustacean	Genus	Phronimidae	Phronimella	1	Phronima	10
Invertebrate	Crustacean	Genus	Trichoniscidae	Haplophthalmus + Oritoniscus	76	Trichoniscus	125
Invertebrate	Mollusc	Family	Cerithioidea	Paludomidae	104	Thiaridae	289
Invertebrate	Mollusc	Family	Corbiculacea	Cyrenidae	234	Sphaeriidae	263
Invertebrate	Mollusc	Genus	Ancylini	Ferrissia	60	Ancylus	31
Invertebrate	Mollusc	Genus	Mytilidae	Perna + Perumytilus + Rhomboidella + Semimytilus + Septifer + Volsellina + Crenomytilus	75	Mytilus	111
Invertebrate	Mollusc	Genus	Bulinini	Indoplanorbis	1	Bulinus	61
Invertebrate	Mollusc	Genus	Planorbinae	Ceratophallus	1	Gyraulus	242
Invertebrate	Mollusc	Genus	Sphaeriidae	Sphaerium	60	Pisidium	161
Invertebrate	Mollusc	Genus	Physini	Physella	16	Physa	60
Invertebrate	Mollusc	Genus	Thiaridae	Tarebia + Thiara	77	Melanoides	98
Invertebrate	Mollusc	Genus	Tateidae	Sororipyrgus	3	Potamopyrgus	35

Table 5.1 Clades used in the analysis of the diversity of polyploid clades continued (3)

Group	Subgroup	Taxonomic Level	Parent Clade	Non-Polyploid Clade	Number of Species	Polyploid Clade	Number of Species
Angiosperm	Basal Angiosperm	Family	Austrobaileyales	Trimeniaceae	12	Illiciaceae + Schisandraceae	73
Angiosperm	Magnolid + Chloranthales	Family	Laurales 1	Monimiaceae	135	Lauraceae	3028
Angiosperm	Magnolid + Chloranthales	Family	Laurales 2	Siparunaceae + Atherospermataceae + Gomortegaceae + Hernandiaceae + Monimiaceae + Lauraceae	3286	Calycanthaceae	11
Angiosperm	Magnolid + Chloranthales	Family	Magnoliales 1	Degeneriaceae + Himantandraceae	3	Magnoliaceae	251
Angiosperm	Magnolid + Chloranthales	Family	Magnoliales 2	Eupomatiaceae	3	Annonaceae	3342
Angiosperm	Magnolid + Chloranthales	Family	Canellales	Canellaceae	24	Winteraceae	163
Angiosperm	Magnolid + Chloranthales	Sub family	Piperaceae	Zippelioideae	7	Piperoideae	4719
Angiosperm	Magnolid + Chloranthales	Genus	Magnolieae	Michelia	23	Magnolia	272
Angiosperm	Magnolid + Chloranthales	Genus	Chloranthaceae	Sarcandra	4	Chloranthus	20
Angiosperm	Magnolid + Chloranthales	Genus	Aristolochioideae	Pararistolochia	10	Aristolochia	487
Angiosperm	Dicot	Family	Basal Eudicots	Buxaceae	123	Trochodendraceae	2
Angiosperm	Dicot	Family	Proteales	Proteaceae	1323	Platanaceae	27
Angiosperm	Dicot	Family	Malpighiales	Lacistemataceae	13	Salicaceae	1275
Angiosperm	Dicot	Family	Sapindales	Simaroubaceae	121	Sapindaceae	1759
Angiosperm	Dicot	Genus	Saxifragales				
Angiosperm	Dicot	Genus	Brassicaceae 1	Catolobus	1	Arabidopsis	16
Angiosperm	Dicot	Genus	Brassicaceae 2	Iodanthus	2	Cardamine	236
Angiosperm	Dicot	Genus	Brassicaceae 3	Cakile	7	Brassica	39
Angiosperm	Dicot	Genus	Brassicaceae 4	Dimorphocarpa	5	Physaria	107
Angiosperm	Dicot	Genus	Brassicaceae 5	Rapistrum + Diplotaxis	39	Crambe	39
Angiosperm	Dicot	Genus	Brassicaceae 6	Rytidocarpus	1	Moricandia	8
Angiosperm	Dicot	Genus	Brassicaceae 7	Athysanus + Heterodraba	2	Draba	400
Angiosperm	Dicot	Genus	Brassicaceae 8	Barbarea	29	Rorippa	91
Angiosperm	Dicot	Genus	Brassicaceae 9	Catalobus	1	Capsella	9
Angiosperm	Dicot	Genus	Brassicaceae 10	Selenia	5	Leavenworthia	9
Angiosperm	Dicot	Genus	Caricaceae	Jacaratia + Vasconcellea	13	Carica	1
Angiosperm	Dicot	Genus	Coffeeae	Calycosiphonia + Argocoffeopsis + Diplospora + Belonophora + Discospermum	48	Coffea	124
Angiosperm	Dicot	Genus	Gossypieae	Gossypioides + Kokia	7	Gossypium	54

Table 5.1 Clades used in the analysis of the diversity of polyploid clades continued (4)

Group	Subgroup	Taxonomic Level	Parent Clade	Non-Polyploid Clade	Number of Species	Polyploid Clade	Number of Species
Angiosperm	Dicot	Genus	Nicotianeae	Anthocercis + Anthotroche + Crenidium + Cyphanthera + Duboisia + Grammosolen + Symonanthus	30	Nicotiana	55
Angiosperm	Dicot	Genus	Solaneae	Jaltomata	35	Solanum	1199
Angiosperm	Dicot	Genus	Diocleae	Cleobulia + Cymbosema + Dioclea + Macropsychanthus + Bionia + Camptosema + Collaea + Cratylia + Galactia + Lackeya + Neorudolphia + Rhodopis	222	Canavalia	70
Angiosperm	Dicot	Genus	Primulaceae	Dionysia	54	Primula	392
Angiosperm	Dicot	Genus	Senecioneae	Chersodoma	9	Senecio	1587
Angiosperm	Dicot	Genus	Vaccinieae	Orthaea+Notopora	39	Vaccinium	223
Angiosperm	Dicot	Genus	Crassulaceae	Monanthes	12	Aichryson	18
Angiosperm	Dicot	Genus	Gesneriaceae	Koellikeria + Gloxinia + Diastema + Monopyle + Kohleria + Pearcea + Phinaea + Moussonia + Smithiantha + Eucodonia + Niphaea	130	Achimenes	26
Angiosperm	Dicot	Genus	Primulaceae	Primula	392	Dodecatheon	15
Angiosperm	Dicot	Genus	Plantaginaceae	Erinus	2	Digitalis+Isoplexis	26
Angiosperm	Dicot	Genus	Mentheae	Cyclotrichium	9	Mentha	42
Angiosperm	Dicot	Genus	Sileneae	Lychnis	14	Silene	488
Angiosperm	Dicot	Family	Apiaceae	Cryptotaenia + Oxypolis + Sium + Cicuta + Oenanthe	58	Perideridia	15
Angiosperm	Dicot	Family	Heliantheae	Baeriopsis + Amblyopappus	2	Lasthenia	19
Angiosperm	Dicot	Family	Microseridinae	Uropappus	3	Microseris	43
Angiosperm	Dicot	Family	Spermacoceae	Stenaria	6	Houstonia	23
Angiosperm	Dicot	Genus	Phrymaceae	Glossostigma + Peplidium	16	Mimulus	155
Angiosperm	Dicot	Genus	Veroniceae	Paederota	7	Veronica	198
Angiosperm	Dicot	Genus	Onagreae	Camissonia	23	Gaura	90
Angiosperm	Dicot	Genus	Anthemideae	Anacyclus + Matricaria	37	Achillea	151
Angiosperm	Dicot	Genus	Coreopsideae	Bidens	249	Coreopsis	100
Angiosperm	Dicot	Genus	Hypochaeridinae	Scorzoneroides	25	Hypochaeris + Leontodon + Helminthotheca + Picris	230
Angiosperm	Dicot	Genus	Machaerantherinae	Oonopsis	4	Machaeranthera	27
Angiosperm	Dicot	Genus	Campanulaceae	Trachelium	3	Campanula sect. Isophylla	441

Table 5.1 Clades used in the analysis of the diversity of polyploid clades continued (5)

Group	Subgroup	Taxonomic Level	Parent Clade	Non-Polyploid Clade	Number of Species	Polyploid Clade	Number of Species
Angiosperm	Dicot	Genus	Ehretioideae	Bourreria	56	Tiquilia	28
Angiosperm	Dicot	Genus	Hydrophylloideae	Romanzoffia	5	Phacelia	186
Angiosperm	Dicot	Genus	Adoxaceae	Sambucus	30	Viburnum	169
Angiosperm	Dicot	Genus	Actinidiaceae	Saurauia + Clematoclethra	103	Actinidia	76
Angiosperm	Dicot	Genus	Polemoniaceae	Gilia + Navarettia	70	Collomia	15
Angiosperm	Dicot	Genus	Geraniaceae	Erodium + Geranium + Monsonia + Sarcocaulon	582	Pelargonium	1697
Angiosperm	Dicot	Genus	Orobanchaceae	Epifagus + Conopholis + Boschniakia	7	Orobanche	119
Angiosperm	Dicot	Genus	Cheloneae	Chelone + Nothochelone	6	Penstemon	301
Angiosperm	Dicot	Genus	Antirrhineae	Neogaerrhinum + Sairocarpus + Mohavea + Galvezia	21	Antirrhinum	21
Angiosperm	Dicot	Genus	Physalinae	Margaranthus	2	Physalis	126
Angiosperm	Dicot	Genus	Montiaceae	Lewisia	17	Claytonia + Montia + Neopaxia	35
Angiosperm	Dicot	Genus	Gunneraceae	Myrothamnus	2	Gunnera	69
Angiosperm	Dicot	Genus	Polemoniaceae	Mitella + Conimitella + Heuchera + Tiarella + Elmera + Tolmiea + Lithophragma + Bensoniella	96	Saxifraga	450
Angiosperm	Dicot	Genus	Lepidieae	Iberis + Capsella	38	Lepidium	234
Angiosperm	Dicot	Genus	Cucurbitaceae	Muellerargia	1	Cucumis	52
Angiosperm	Dicot	Genus	Fabeae	Pisum	7	Lathyrus	186
Angiosperm	Dicot	Genus	Betulaceae	Alnus	46	Betula	121
Angiosperm	Dicot	Genus	Malvoideae	Nototriche	94	Tarasa	27
Angiosperm	Dicot	Genus	Lythraceae	Woodfordia	2	Cuphea	280
Angiosperm	Dicot	Genus	Circaeeae	Circaea	15	Fuschia	110
Angiosperm	Dicot	Genus	Rosoideae	Waldsteinia	4	Geum & allies	35
Angiosperm	Dicot	Genus	Selineae	Lomatium	87	Angelica	116
Angiosperm	Dicot	Genus	Gnaphalieae	Leontopodium	61	Antennaria	61
Angiosperm	Dicot	Genus	Apiaceae	Apiaceae	3257	Bupleurum	208
Angiosperm	Dicot	Genus	Asteraceae	Calotis	27	Aster	234
Angiosperm	Dicot	Genus	Senecioneae	Senecio + Lopholaena + Blennosperma + Syneilesis	1613	Doronicum	39
Angiosperm	Dicot	Genus	Ericaceae	Bryanthus + Empetrum	4	Kalmia	10
Angiosperm	Dicot	Genus	Apiaceae	Eyngium	250	Sanicula	44
Angiosperm	Dicot	Genus	Aralieae	Aralia	74	Panax	12
Angiosperm	Dicot	Genus	Aralioideae	Trevesia	11	Hedera	18
Angiosperm	Dicot	Genus	Asclepiadoideae	Stapelia	56	Ceropegia	217

Table 5.1 Clades used in the analysis of the diversity of polyploid clades continued (6)

Group	Subgroup	Taxonomic Level	Parent Clade	Non-Polyploid Clade	Number of Species	Polyploid Clade	Number of Species
Angiosperm	Dicot	Genus	Anthemideae	Leucanthemella + Eumorphia + Arctanthemum + Crossostephium + Ajania + Tripleurospermum	87	Artemisia	481
Angiosperm	Dicot	Genus	Boraginaceae	Plagiobothrys	79	Amsinckia	14
Angiosperm	Dicot	Genus	Plantaginaceae	Streptocarpus	134	Callitriche	63
Angiosperm	Dicot	Genus	Lobelioideae	Clermontia	24	Lobelia	414
Angiosperm	Dicot	Genus	Caryophyllaceae	Arenaria	273	Moehringia	30
Angiosperm	Dicot	Genus	Betoideae	Hablitzia + Aphanisma + Oreobliton + Patellifolia	4	Beta	9
Angiosperm	Dicot	Genus	Rhodoreae	Ledum	6	Rhododendron	641
Angiosperm	Dicot	Genus	Dalbergieae	Arachis	81	Stylosanthes	46
Angiosperm	Dicot	Genus	Chironieae	Chironia + Orphium	26	Centaurium	31
Angiosperm	Dicot	Genus	Hamamelidaceae	Loropetalum	3	Corylopsis	27
Angiosperm	Dicot	Genus	Lamiaceae	Pycnanthes + Blephilia	6	Monarda	22
Angiosperm	Dicot	Genus	Sanguisorbinae	Cliffortia	105	Sanguisorba	26
Angiosperm	Dicot	Genus	Vellinae	Euzomodendron	3	Vella	7
Angiosperm	Dicot	Genus	Mercurialinae	Discoclaoxylon + Lobanilia + Micrococca + Erythrococca + Claoxylon	178	Mercurialis	14
Angiosperm	Dicot	Genus	Coriariaceae	Francoa + Geranium	418	Coriaria	16
Angiosperm	Dicot	Genus	Gnaphalieae	Helichrysum	506	Raoulia	26
Angiosperm	Dicot	Genus	Didiereaceae	Decarya + Didierea	1	Alluaudia	6
Angiosperm	Dicot	Genus	Cynareae	Carduncellus	4	Carthamus	48
Angiosperm	Monocot	Genus	Andropogoneae	Miscanthus	16	Saccharum	36
Angiosperm	Monocot	Genus	Triticeae	Aegilops	25	Triticum	28
Angiosperm	Monocot	Genus	Musaceae	Ensete	10	Musa	70
Angiosperm	Monocot	Genus	Narcisseae	Sternbergia	9	Narcissus	116
Angiosperm	Monocot	Genus	Hemerocallidoideae	Simethis	1	Hemerocallis	19
Angiosperm	Monocot	Genus	Araceae	Remusatia + Steudnera	13	Colocasia	8
Angiosperm	Monocot	Genus	Allieae	Prototulbaghia + Tulbaghia + Leucocoryneae + Gilliesieae	230	Allium	918
Angiosperm	Monocot	Genus	Dioscoreaceae	Rajania	19	Disoscorea	613
Angiosperm	Monocot	Genus	Tripsacinae	Tripsacum	14	Zea	6
Angiosperm	Monocot	Genus	Agavoideae	Beschorneria + Furcraea	31	Agave	200
Angiosperm	Monocot	Genus	Lilioideae	Lloydia	7	Gagea	209

Table 5.1 Clades used in the analysis of the diversity of polyploid clades continued (7)

Group	Subgroup	Taxonomic Level	Parent Clade	Non-Polyploid Clade	Number of Species	Polyploid Clade	Number of Species
Angiosperm	Monocot	Genus	Triticeae	Elymus	234	Psathyrostachys	10
Angiosperm	Monocot	Genus	Arethuseae	Arethusa + Eleorchis	2	Calopogon	5
Angiosperm	Monocot	Genus	Sorghinae	Chrysopogon + Microstegium + Apluda + Sorghastrum	93	Sorghum	31
Angiosperm	Monocot	Genus	Alismatales	Scheuchzeriaceae + Juncaginaceae + Posidoniaceae + Cymodoceaceae + Ruppiaceae	90	Aponogetonaceae	58
Angiosperm	Monocot	Genus	Arisaemateae	Pinellia	9	Arisaema	180
Angiosperm	Monocot	Genus	Lemnoideae	Spirodela	4	Lemna + Wolffia + Wolffiella	35
Angiosperm	Monocot	Genus	Burmanniaceae	Dioscorea	614	Burmannia + Gymnosiphon + Apteria + Cymbocarpa + Hexapterella + Dictyostega	92
Angiosperm	Monocot	Genus	Trilliaceae	Pseudotrillium	1	Trillium + Paris	77
Angiosperm	Monocot	Genus	Oryzinae	Leersia	18	Oryza	18
Angiosperm	Monocot	Genus	Galantheae	Leucojum	2	Galanthus	21
Angiosperm	Monocot	Genus	Amaryllidaceae	Habranthus	83	Zephyranthes	88
Angiosperm	Monocot	Genus	Iridaceae	Sparaxis	15	Iris	362
Angiosperm	Monocot	Genus	Asparagoideae	Hemiphylacus	5	Asparagus	211
Angiosperm	Monocot	Genus	Poeae	Helictotrichon	90	Avena	22
Angiosperm	Monocot	Genus	Pooideae	Phalaris	19	Briza	22
Angiosperm	Monocot	Genus	Medeoloideae	Medeola	1	Clintonia	5
Non-angiosperm	Gymnosperm	Genus	Gnetophytes	Gnetum	42	Ephedra	70
Non-angiosperm	Gymnosperm	Genus	Sequoioideae	Metasequoia	5	Sequoia	6
Non-angiosperm	Gymnosperm	Genus	Callitroideae	Diselma	2	Fitzroya	2
Non-angiosperm	Gymnosperm	Genus	Cupressoideae	Xanthocyparis	2	Cupressus + Juniperus	95
Non-angiosperm	Gymnosperm	Genus	Podocarpaceae 1	Falcatifolium	7	Dacrydium	28
Non-angiosperm	Gymnosperm	Genus	Podocarpaceae 2	Nageia + Afrocarpus + Retrophyllum	17	Podocarpus	120

Table 5.1 Clades used in the analysis of the diversity of polyploid clades continued (8)

Group	Subgroup	Taxonomic Level	Parent Clade	Non-Polyploid Clade	Number of Species	Polyploid Clade	Number of Species
Non-angiosperm	Fern	Genus	Polypodiales	Hemidictyaceae	1	Aspleniaceae	517
Non-angiosperm	Fern	Genus	Blechnaceae	Woodwardia	27	Blechnum	148
Non-angiosperm	Fern	Genus	Cyatheaceae	Alsophila	71	Cyathea	320
Non-angiosperm	Fern	Genus	Dennstaedtiaceae 1	Leptolepia	1	Dennstaedtia + Microlepia	123
Non-angiosperm	Fern	Genus	Dennstaedtiaceae 2	Saccoloma + Paesia + Blotiella + Histiopteris	34	Hypolepis	52
Non-angiosperm	Fern	Genus	Dennstaedtiaceae 3	Odontosoria	14	Sphenomeris	8
Non-angiosperm	Fern	Genus	Dryopteridaceae 1	Leptorumohra + Phanerophlebiopis + Lithostegia	15	Arachniodes	138
Non-angiosperm	Fern	Genus	Dryopteridaceae 2	Cyrtogonellum	8	Cyrtomium	43
Non-angiosperm	Fern	Genus	Dryopteridaceae 3	Acrorumohra + Peranema + Diacalpe + Acrophorus	26	Dryopteris	305
Non-angiosperm	Fern	Genus	Dryopteridaceae 4	Cyrtogonellum	8	Polystichum	276
Non-angiosperm	Fern	Genus	Dryopteridaceae 5	Megalastrum	55	Rumohra	5
Non-angiosperm	Fern	Genus	Dryopteridaceae 6	Prosaptia	3	Tectaria	195
Non-angiosperm	Fern	Genus	Dryopteridaceae 7	Cheilanthopsis + Peranema	5	Woodsia	43
Non-angiosperm	Fern	Genus	Physematieae	Pseudocystopteris	7	Athyrium	216
Non-angiosperm	Fern	Genus	Cystopteridaceae	Acystopteris	3	Cystopteris + Gymnocarpium	35
Non-angiosperm	Fern	Genus	Athyriaceae	Anisocampium + Cornopteris	18	Diplazium	211
Non-angiosperm	Fern	Genus	Hymenophyllaceae 1	Pachychaetum	10	Cephalomanes	12
Non-angiosperm	Fern	Genus	Hymenophyllaceae 2	Crepidomanes	32	Gonocormus	2
Non-angiosperm	Fern	Genus	Hymenophyllaceae 3	Didymoglossum + Trichomanes	139	Abrodictyum	10
Non-angiosperm	Fern	Genus	Hymenophyllaceae 4	Hymenophyllum	172	Sphaerocionium	10
Non-angiosperm	Fern	Genus	Lycopodiophyta	Lycopodiopsida	475	Isoetopsida	1008
Non-angiosperm	Fern	Genus	Elaphoglossoideae	Teratophyllum + Lomagramma	19	Elaphoglossum	584
Non-angiosperm	Fern	Genus	Lomariopsidaceae	Cyclopeltis	3	Lomariopsis	35
Non-angiosperm	Fern	Genus	Lycopodiaceae 1	Dendrolycopodium	4	Diphasiastrum	21
Non-angiosperm	Fern	Genus	Lycopodiaceae 2	Phylloglossum	1	Huperzia	250

Table 5.1 Clades used in the analysis of the diversity of polyploid clades continued (9)

Group	Subgroup	Taxonomic Level	Parent Clade	Non-Polyploid Clade	Number of Species	Polyploid Clade	Number of Species
Non-angiosperm	Fern	Genus	Lycopodiaceae 3	Pseudolycopodiella + Palhinhaea	10	Lycopodiella	30
Non-angiosperm	Fern	Genus	Lycopodiaceae 4	Spinulum	3	Lycopodium	70
Non-angiosperm	Fern	Genus	Marattiaceae	Angiopteris	75	Marattia	60
Non-angiosperm	Fern	Genus	Marsileaceae	Regnellidium + Pilularia	9	Marsilea	111
Non-angiosperm	Fern	Genus	Polypodiineae	Blechnoideae	246	Oleandraceae	80
Non-angiosperm	Fern	Genus	Ophioglossaceae 1	Helminthostachys	6	Botrychium + Botrypus + Sceptridium	132
Non-angiosperm	Fern	Genus	Ophioglossaceae 2	Ophioderma + Cheiroglossa	16	Ophioglossum	118
Non-angiosperm	Fern	Genus	Cyatheales	Culcitaceae	6	Plagiogyriaceae	20
Non-angiosperm	Fern	Genus	Polypodiaceae 1	Niphidium	14	Campyloneurum	74
Non-angiosperm	Fern	Genus	Polypodiaceae 2	Drymotaenium	1	Lepisorus	140
Non-angiosperm	Fern	Genus	Polypodiaceae 3	Anarthropteris	2	Loxogramme	70
Non-angiosperm	Fern	Genus	Polypodiaceae 4	Niphidium + Campyloneurum	74	Microgramma	38
Non-angiosperm	Fern	Genus	Polypodiaceae 5	Lecanopteris + Leptochilus	130	Microsorum	118
Non-angiosperm	Fern	Genus	Polypodiaceae 6	Calymmodon + Prosaptia + Grammitis + Themelium + Micropolypodium + Terpsichore + Adenophorus	590	Polypodium	1356
Non-angiosperm	Fern	Genus	Microsoreae	Leptochilus	114	Colysis	77
Non-angiosperm	Fern	Genus	Drynarioideae	Polypodiopteris	3	Selliguea	124
Non-angiosperm	Fern	Genus	Platycerioideae	Platycerium	27	Pyrrosia	109
Non-angiosperm	Fern	Genus	Pteridoideae	Cosentinia	2	Anogramma + Pityrogramma	116
Non-angiosperm	Fern	Genus	Pteridaceae 1	Pteridoideae	1075	Ceratopteridoideae	322
Non-angiosperm	Fern	Genus	Pteridaceae 2	Sinopteris	3	Aleuritopteris	63
Non-angiosperm	Fern	Genus	Pteridaceae 3	Cheilanthes	375	Argyrochosma + Pellaea + Platyloma	147
Non-angiosperm	Fern	Genus	Pteridaceae 4	Cheilanthes	375	Aspidotis	5
Non-angiosperm	Fern	Genus	Pteridaceae 5	Llavea	1	Cryptogramma + Coniogramme	85

Table 5.1 Clades used in the analysis of the diversity of polyploid clades continued (10)

Group	Subgroup	Taxonomic Level	Parent Clade	Non-Polyploid Clade	Number of Species	Polyploid Clade	Number of Species
Non-angiosperm	Fern	Genus	Pteridaceae 6	Cheilanthes	375	Doryopteris	92
Non-angiosperm	Fern	Genus	Pteridaceae 7	Pterozonium + Taenitis	55	Jamesonia	60
Non-angiosperm	Fern	Genus	Pteridaceae 8	Adiantopsis + Cheilanthes + Doryopteris	504	Hemionitis	47
Non-angiosperm	Fern	Genus	Pteridaceae 9	Actiniopteris	8	Onychium	23
Non-angiosperm	Fern	Genus	Pteridaceae 10	Platyloma	1	Pellaea	130
Non-angiosperm	Fern	Genus	Pteridaceae 11	Ochropteris	2	Pteris	779
Non-angiosperm	Fern	Genus	Salviniaceae	Azolla	14	Salvinia	29
Non-angiosperm	Fern	Genus	Schizaeaceae 1	Actinostachys + Schizaea	85	Anemia + Mohria	185
Non-angiosperm	Fern	Genus	Schizaeaceae 2	Microschizaea	7	Schizaea	56
Non-angiosperm	Fern	Genus	Thelypteridaceae 1	Metathelypteris	19	Amauropelta	23
Non-angiosperm	Fern	Genus	Thelypteridaceae 2	Amphineuron	11	Christella + Sphaerostephanos + Pronephrium	378
Non-angiosperm	Fern	Genus	Thelypteridaceae 3	Ampelopteris + Mesophlebion	21	Cyclosorus	526
Non-angiosperm	Fern	Genus	Vittariaceae	Anetium	3	Antrophyum + Polytaenium + Vittaria	242
Non-angiosperm	Fern	Genus	Hymenophyllaceae	Vandenboschia	34	Didymoglossum	75

Table 5.1 Clades used in the analysis of the diversity of polyploid clades continued (11)

Although the dataset included clades at a range of different taxonomic ranks, 321 of the 356 clade pairs were genera. All of the remaining 35 clade pairs were at taxonomic ranks above genus, with 28 pairs of families, 4 pairs of subfamilies, 2 pairs of orders and 1 pair of suborders. Unlike the larger genera-level dataset, most of the supra-generic clades (24 out of 35) were from animals, with only 9 clade pairs from plants. The majority of the supra-generic animal clades were fishes (16 clade pairs), with 3 annelid clade pairs, 2 mollusc clade pairs, 2 insect clade pairs and 1 lissamphibian clade. Of the supra-generic plant clades, 6 clade pairs were from the magnolids and chloranthales clade, 4 clade pairs were from dicots and 1 clade pair from Austrobaileyales. As most clade pairs were genera, taxonomic overlap was almost non-existant, however analyses were still performed on each taxonomic level seperately to rule out this effect.

5.3.2 Comparing The Diversity Of Polyploid & Non-polyploid Clades Across The Whole Dataset

Paired Wilcoxon signed-rank tests showed that the polyploid clades had significantly more species than their non-polyploid sister clades, with p-values less than 0.001 in many cases (**Table 5.2**). Generally speaking, analyses on groups with larger sample sizes produced a more significant difference (lower p-values) than the smaller samples. Of the larger subclades, only tetrapods were non-significant (n = 49, V = 767.5, p-value = 0.066). Several subclades with smaller sample sizes were also non-significant, namely lissamphibians (n = 29, V = 285.5, p-value = 0.062), reptiles (n = 17, V = 91, p-value = 0.507), annelid worms (n = 13, V = 67, p-value = 0.142), the magnoliid and Chloranthales clade (n = 9, 767.5, p-value = 0.066), monocots (n = 27, 251.5, p-value = 0.055) and gymnosperms (n = 6, V = 15, p-value = 0.060).

Dataset	Number of Clade Pairs	Wilcoxon signed-rank V	P-Value
All	356	45769	6.734×10^{-16}
Animals	153	8825	9.807×10^{-9}
Plants	203	14468	1.072×10^{-8}
Vertebrates	91	3028	8.032×10^{-5}
Invertebrates	62	1542	7.445×10^{-5}
Angiosperms	128	5501.5	5.018×10^{-5}
Non-angiosperms	75	2155	3.595×10^{-5}
Tetrapods	49	767.5	0.066
Fish	42	2155	1.802×10^{-4}
Lissamphibians	29	285.5	0.062
Reptiles	17	91	0.507
Insects	32	386.5	0.022
Annelids	13	67	0.142
Crustaceans	6	21	0.036
Molluscs	10	52.5	0.012
Magnoliids + Chloranthales	9	767.5	0.066
Dicots	91	2654.5	0.004
Monocots	27	251.5	0.055
Gymnosperms	6	15	0.060
Ferns	69	1852	1.179×10^{-4}

Table 5.2 Two-tailed paired Wilcoxon signed-rank tests on the clade pairs of all taxonomic ranks, for the entire dataset (All) as well as clade pairs in each subgroup.

Fairly similar patterns were found for both animals and plants as a whole, as well as the major groups within them (**Fig. 5.1**). In animals, the most speciose polyploid clade contained 82,320 taxa, while the smallest clades contained only a single species (mean = 649, median = 38.8). Non-polyploid clades contained significantly fewer species (V = 8825, p-value = 9.807×10^{-9}), the largest clade containing only 1,758 species and many clades having species counts below 100 (mean = 67, median = 14.5). Examining box plots of polyploid and non-polyploid clades for animals (**Fig. 5.1**, panel A) shows that although the two samples had quite similar distributions, the polyploid sample had a greater number of highly speciose outlier clades, even with the much more diverse Curculionidae removed. The higher species counts in polyploid clades are also clearly evident in the difference plot, with few points below the zero line. Plants also showed a highly significant difference between polyploid and non-polyploid clades (V = 14,468, p-value =1.072×10^{-8}), while both samples had clades with one species, the species counts of polyploid clades (maximum = 4,719, mean = 220, median = 70) were substantially higher than the non-polyploid sample (maximum = 3,286, mean = 112, median = 15). Like animals, most of the highly speciose outliers were in the polyploid sample (**Fig. 5.1**, panel B) although non-polyploids also contained anomalously speciose clades. This produced a slightly more even distribution of outlier values around the zero line even though most differences were still positive. Within animals, vertebrates and invertebrates showed patterns similar to those found in animals as a whole, with both clades showing highly significant differences (vertebrates: V = 3028, p-value = 8.032×10^{-5}, invertebrates: V = 1,542, p-value = 7.445×10^{-5}). For vertebrates, polyploid clades (maximum = 990, mean = 83, median = 25) were generally more speciose than their polyploid counterparts (maximum = 630, mean = 44, median = 12) as well as having a larger number of highly speciose outliers (**Fig. 5.1**, Panel C). Invertebrates showed an even greater difference between polyploid (maximum = 82,320, mean = 1,489, median = 60) and non-polyploid (maximum = 1,758, mean = 102, median = 25) clades, with fewer high value outliers in the non-polyploid sample (**Fig. 5.1**, Panel D). Both vertebrates and invertebrates showed more values within the upper and lower quartile bounds (shown by the larger size of the boxes in these plots) and fewer values outside the 95% confidence interval 'whiskers'. Finally, within plants the angiosperms showed a pattern very like plants as a whole and polyploid clades are again much more speciose (maximum = 4,719, mean = 257, median = 57) than non-polyploid ones (maximum = 3,286, mean = 133, median = 18). While most difference values were positive, there were also some highly negative difference values due to highly speciose non-polyploid clades (**Fig. 5.1**, panel E). The other plant groups studied also showed this tendency to have a few highly speciose non-polyploid clades (**Fig. 5.1**, panel F) although again, species numbers in polyploid clades (maximum = 1,356, mean = 160, median = 75) were

generally much higher than in non-polyploid ones (maximum = 1,075, mean = 76, median = 11). Wilcoxon signed-rank tests showed these differences were highly significant for both angiosperms (V = 5,501.5, p-value = 5.018×10^{-5}) and non-angiosperm plant groups (V = 2,155, p-value = 3.595×10^{-5}).

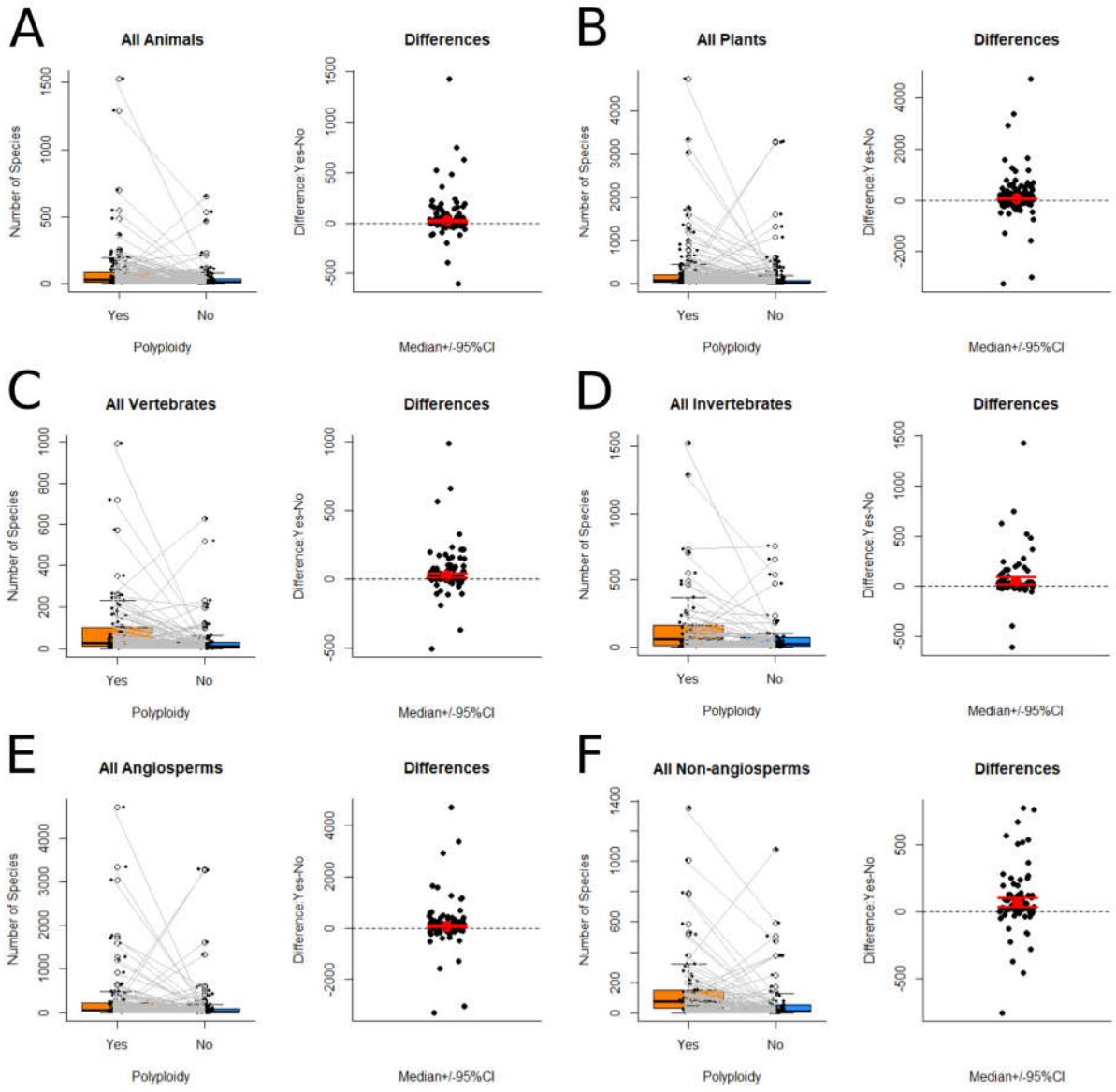

Fig. 5.1 Boxplots of raw values and differences in number of species between polyploid and non-polyploid clades at all taxonomic levels for major groups of plants and animals. Boxes delimit the upper and lower quartiles of the data, while central bars are median values. Whiskers delimit plus or minus 1.5 times the inter-quartile range, from the first and third quartiles. Grey lines connect pairs of values from the same clade. Differences given are values from polyploid minus non-polyploid clades, with positive differences indicating higher values in sample of polyploid clades. In the null case, difference values would be randomly distributed around the estimated pseudomedian shown in red, with upper and lower 95% confidence intervals.

Looking at subgroups within these larger animal groups showed greater variability both in terms of the spread of data and the magnitude of the differences between polyploid and non-polyploid clades. Tetrapods (**Fig. 5.2**, panel A) differed from the pattern seen in vertebrates as a whole by having some non-polyploid clades with very high numbers of species, skewing the distribution of differences to be more towards the zero line than it would otherwise be. Although polyploid clades in tetrapods still showed slightly higher numbers of species (maximum = 256, mean = 36, median = 14) than non-polyploid clades (maximum = 520, mean = 34, median = 10), this difference was not significant (V = 767.5, p-value = 0.066) as it was for polyploid (maximum = 1356, mean = 169, median = 77) and non-polyploid (maximum = 1075, mean = 82, median = 14) clades of fishes (V = 2155, p-value = 1.802×10^{-4}). While fishes contained a number of clades with high numbers of species in both samples (**Fig. 5.2**, panel B), difference values were positively skewed relative to the estimated pseudomedian. In tetrapods, the distribution of these differences was skewed towards the centre due to high species counts in some tetrapod non-polyploid clades (**Fig. 5.2**, panel A). In fact, non-polyploid clades showed a higher number of species, despite having lower average values. Patterns within lissamphibians (**Fig. 5.2**, panel C) were essentially the same as within the larger tetrapod dataset (polyploid: maximum = 192, mean = 32, median = 15, non-polyploid: maximum = 520, mean = 34, median = 9, Wilcoxon: V = 285.5, p-value = 0.062) while reptiles (**Fig. 5.2**, panel D) showed little difference in the number of species between polyploid and non-polyploid clades (V = 91, p-value = 0.507). Average numbers of species in polyploid reptile clades was only slightly higher (maximum = 256, mean = 48, median = 24) than in non-polyploid clades (maximum = 232, mean = 38, median = 15) and difference values were distributed fairly evenly around the pseudomedian.

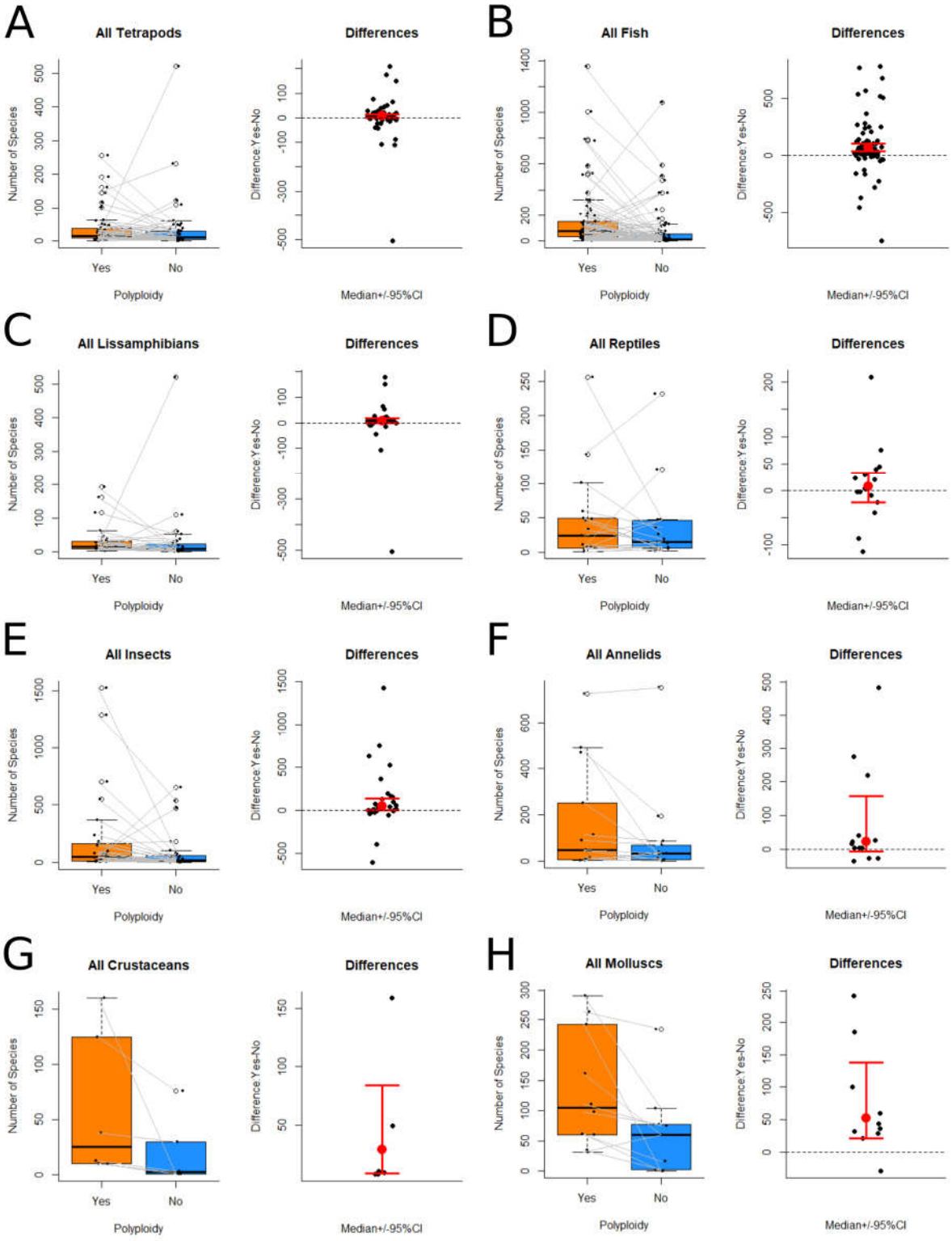

Fig. 5.2 Boxplots of raw values and differences in number of species between polyploid and non-polyploid clades in animal subgroups at all taxonomic levels

Within the invertebrates, insects showed patterns most similar to the combined invertebrate sample (**Fig. 5.2**, panel E), which is unsurprising given that the majority of invertebrate clades analysed were insects. Polyploid clades of insects (maximum = 82,320, mean = 2,760, median = 55) had on average at least twice the numbers of species of non-polyploid clades (maximum = 1758, mean = 134, median = 21) and showed both a greater number of positive outliers in the polyploid sample, a greater range of values and positively skewed differences which were highly significant (V = 386.5, p-value = 0.022). The other invertebrate subclades, namely annelid worms (**Fig. 5.2**, panel F), crustaceans (**Fig. 5.2**, panel G) and molluscs (**Fig. 5.2**, panel H) all showed similar differences between their polyploid and non-polyploid clade samples. In each case, the samples of polyploid clades showed a much greater range of values than non-polyploid samples and differences between most clades are positive relative to the pseudo-median. In crustaceans (polyploid: maximum = 160, mean = 59, median = 26, non-polyploid: maximum = 76, mean = 19, median = 3, Wilcoxon: V = 21, p-value = 0.036) and molluscs (polyploid: maximum = 289, mean = 135, median = 105, non-polyploid: maximum = 234, mean = 63, median = 60, Wilcox: V = 52.5, p-value = 0.012) these differences were significant, whilst in annelids (polyploid: maximum = 723, mean = 174, median = 48, non-polyploid: maximum = 750, mean = 97, median = 32, Wilcoxon: V = 67, p-value = 0.142) they were not.

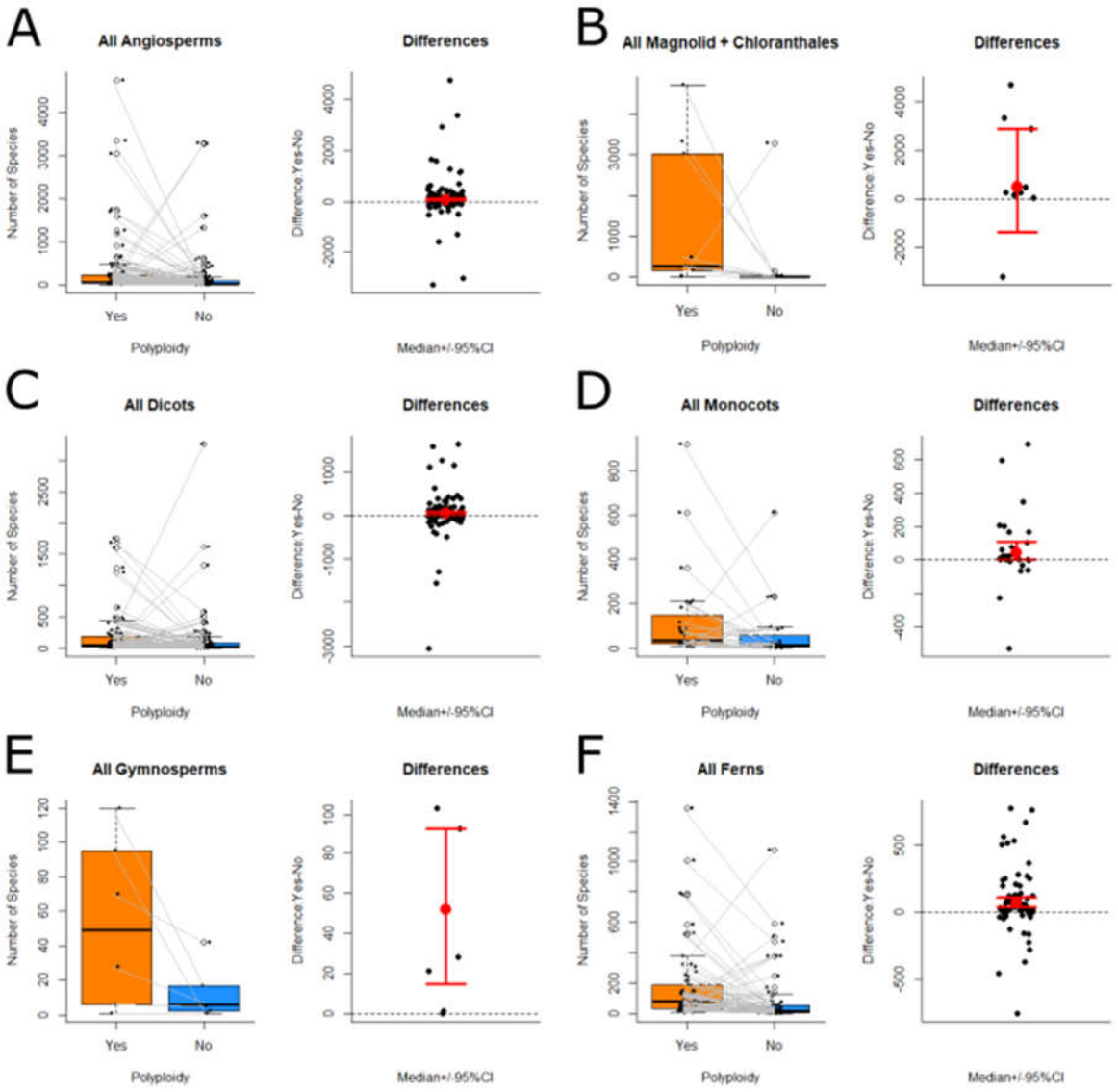

Fig. 5.3 Boxplots of raw values and differences in number of species between polyploid and non-polyploid clades in plant subgroups at all taxonomic levels

Within plants, dicots (V = 2654.5, p-value = 0.004) and ferns (V = 1852, p-value = 1.179 x 10^{-4}) showed significantly higher numbers of species in their polyploid samples than their non-polyploid samples, while monocots (V = 251.5, p-value = 0.055), magnolids and Chloranthales (V = 767.5, p-value = 0.066) and gymnosperms (V = 15, p-value = 0.060) did not (**Table 5.2**). The dicots (**Fig. 5.3**, panel C) showed distributions of values most similar to angiosperms as a whole (**Fig. 5.3**, panel A) with the sample of polyploid clades (maximum = 1,759, mean = 187, median = 52) having a greater range and higher average than the non-polyploid clades (maximum = 3,257, mean = 130, median = 24), although both samples had a roughly equal number of extremely diverse clades. The plot of difference values shows that most values are clustered close to or at slightly positive values relative to the pseudo-median, with a small number of very positive and

very negative difference values. The monocot datatset, as well as being smaller, showed slightly fewer extreme or outlier values (**Fig. 5.3**, panel D). This results in difference values which are more evenly scattered around the pseudo-median, although polyploid clades (maximum = 918, mean = 128, median = 36) were still on average around twice as speciose as non-polyploid ones (maximum = 614, mean = 61, median = 15). Although the number of clade pairs analysed in the clade consisting of the magnolids and chloranthales (**Fig. 5.3**, panel B) was much smaller than either the dicot or monocot samples, polyploid clades had vastly more species (maximum = 4,719, mean = 1,365, median = 272) and a much greater range of species than non-polyploid clades (maximum = 3286, mean = 388, median = 10). Whilst one non-polyploid magnolid clade, Piperoideae, contained an unusually high species count of 3,286, all other non-polyploid clades had less than 150 species, with all but one being under 25 species.

Among the non-angiosperm groups, polyploid (maximum = 120, mean = 53, median = 49) and non-polyploid (maximum = 42, mean = 12, median = 6) clades of gymnosperms both showed relatively low species diversity although, like magnolids, polyploid clades of gymnosperms showed a much greater range of values as well as much higher numbers of species in general (**Fig. 5.3**, panel E). The small size of the gymnosperm dataset led to substantial error when estimating the pseudo-median, with difference values scattered fairly randomly within these error bars, although difference values were all positive (that is to say, no polyploid clade had lower diversity than its non-polyploid sister clade). The sample size for ferns was far larger (**Fig. 5.3**, panel F), with more typical distribution patterns; whilst both polyploid (maximum = 1,356, mean = 169, median = 77) and non-polyploid (maximum = 1,075, mean = 82, median = 14) contained highly diverse clades, species numbers in polyploid clades were generally much higher. This is shown in the difference plot, in which the majority of values are skewed towards positive values relative to the pseudo-median.

Dataset	Number of Clade Pairs	Wilcoxon signed-rank V	P-Value
All	321	36829	5.645×10^{-14}
Animals	129	6150	5.209×10^{-7}
Plants	192	12928	2.351×10^{-8}
Vertebrates	75	1941.5	4.334×10^{-4}
Invertebrates	55	1200.5	3.143×10^{-4}
Angiosperms	177	4556.5	1.302×10^{-4}
Non-angiosperms	75	2155	3.595×10^{-5}
Tetrapods	48	767.5	0.032
Fish	26	263	0.007
Lissamphibians	28	285.5	0.021
Reptiles	17	91	0.507
Insects	30	338.5	0.030
Annelids	10	40	0.221
Crustaceans	6	21	0.036
Molluscs	8	34	0.023
Magnoliids + Chloranthales	3	6	0.250
Dicots	87	2457.5	0.003
Monocots	27	251.5	0.055
Gymnosperms	6	15	0.059
Ferns	69	1852	1.179×10^{-4}

Table 5.3 Two-tailed paired Wilcoxon signed-rank tests on pairs of genera, for the entire dataset (All) as well as clade pairs in each subgroup.

5.3.2 Comparing The Diversity Of Polyploid & Non-polyploid Clades At The Generic Level

Separate analyses on the sample of genera included in the study were, unless otherwise stated, in agreement with those of the larger combined dataset (**Table 5.3**). From the larger groups, polyploid and non-polyploid clades in animals (**Fig. 5.4**, panel A), invertebrates (**Fig. 5.4**, panel D), angiosperms (**Fig. 5.4**, panel E) and non-angiosperms (**Fig. 5.4**, panel F) all showed patterns essentially identical to the complete dataset analyses with slightly fewer data. Polyploid genera in plants (maximum = 1,697, mean = 157, median = 66) had slightly lower average and maximum values relative to non-polyploid clades (maximum = 3,257, mean = 92, median = 15) than the complete dataset due to the absence of some of the most speciose non-polyploid clades (**Fig. 5.4**, panel B). This can be seen in the difference plot, where the most extreme negative outliers are no longer present. In vertebrates (**Fig. 5.4**, panel C) although both polyploid (maximum = 256, mean = 46, median = 16) and non-polyploid (maximum = 232, mean = 24, median = 10) maximums and averages were much lower for the generic dataset, polyploid clades were still significantly more speciose ($V = 1941.5$, p-value = <0.001). A few of the vertebrate clade pairs of higher taxonomic rank (which were not included in the genera

subsample) had non-polyploid clades with very high numbers of species, therefore while average number of species in polyploid clades was lower, the distribution of differences relative to the pseudo-median was similar to the complete dataset.

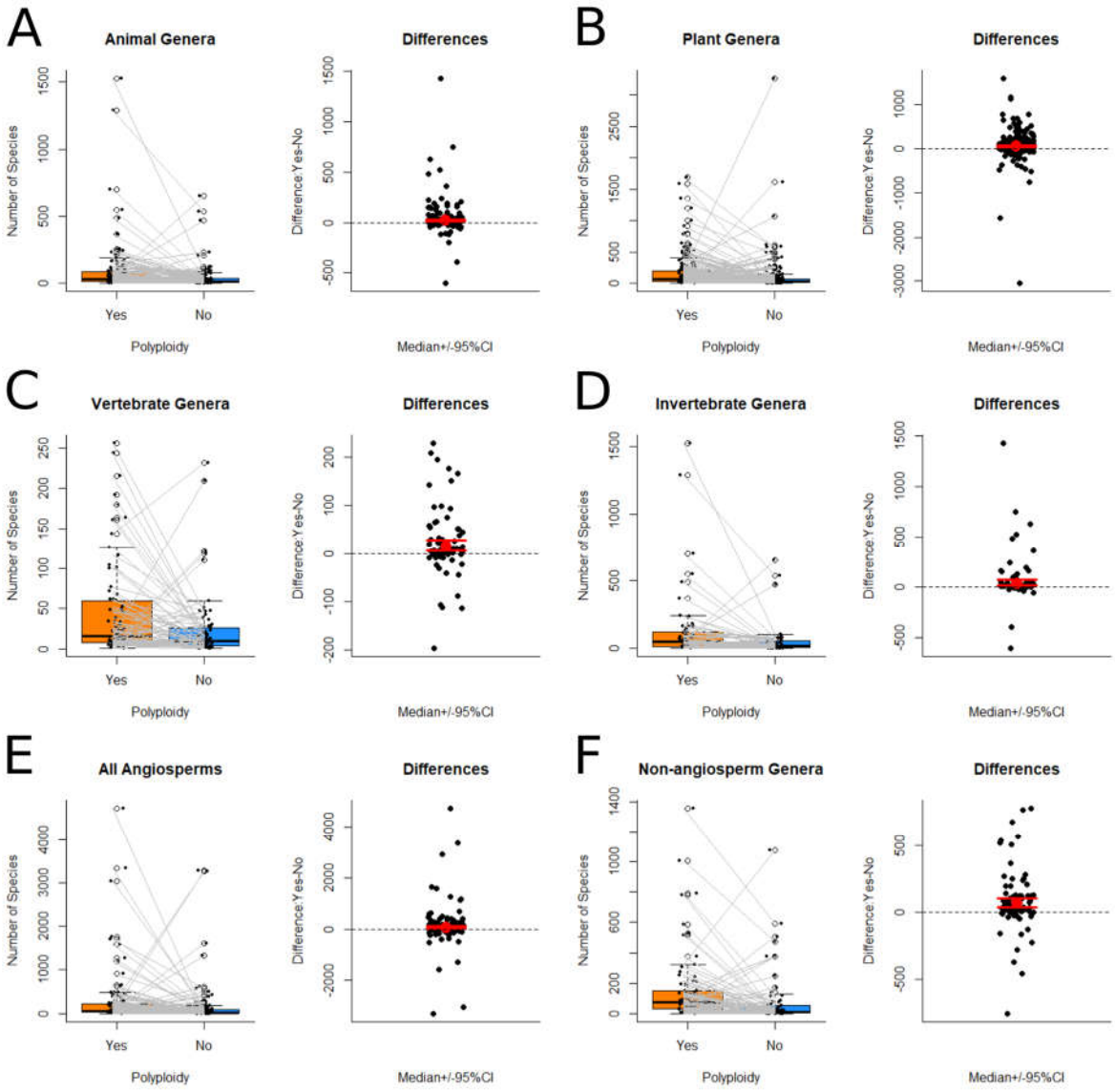

Fig. 5.4 Boxplots of raw values and differences in number of species between polyploid and non-polyploid genera for major groups of plants and animals. Boxes delimit the upper and lower quartiles of the data, while central bars are median values. Whiskers delimit plus or minus 1.5 times the inter-quartile range, from the first and third quartiles. Grey lines connect pairs of values from the same clade. Differences given are values from polyploid minus non-polyploid clades, with positive differences indicating higher values in sample of polyploid clades. In the null case, difference values would be randomly distributed around the estimated pseudomedian shown in red, with upper and lower 95% confidence intervals.

Generic samples within vertebrate subgroups also revealed patterns in broad consilience with those from the entire data set, although some differences which were non-significant in the full dataset proved to be significant in the generic sample. Tetrapods showed a significant difference (V = 767.5, p-value = 0.032) between polyploid (max = 256, mean = 36, median = 13) and non-polyploid clades (max = 232, mean = 24, median = 10) although to a lesser extent than for vertebrates as a whole. Many of the clades with the highest numbers of species were of a higher taxonomic rank and not present in the tetrapod generic dataset, specifically a few non-polyploid clades which were more speciose than their polyploid sister clades (**Fig. 5.5**, panel A). This is largely due to the absence of speciose non-polyploid clades in the lissamphibian sample (**Fig. 5.5**, panel C). As a result, differences between lissamphibian polyploid (max = 192, mean = 33, median = 14) and non-polyploid (max = 110, mean = 17, median = 8) genera were significant in the generic dataset (V = 285.5, p-value = 0.021). Contrastingly, fish showed slightly less of a difference (V = 263, p-value = 0.004) between polyploid (max = 244, mean = 64, median = 43) and non-polyploid (max = 210, mean = 24, median = 11) clades in the generic dataset relative to the complete dataset, with fewer highly speciose outliers (**Fig. 5.5**, panel B). Reptile genera showed a pattern essentially identical to the whole sample of reptile clades (**Fig. 5.5**, panel D) with no significant difference between polyploid (maximum = 256, mean = 48, median = 24) and non-polyploid samples (V = 91, p-value = 0.507).

Invertebrate generic datasets were also very similar to those of the complete dataset, with crustaceans (**Fig. 5.5**, panel G) being identical (V = 21, p-value = 0.036). The distributions and differences between insect generic pairs (**Fig. 5.5**, panel E) were also very similar to the whole dataset (V = 338.5, p-value = 0.030) with the only difference being the removal of the highly speciose weevil superfamily Curculionoidea and the fly family Chamaemyiidae. Genera of annelid worms did not show a significant difference (V = 40, p-value = 0.221) between polyploid (maximum = 488, mean = 82, median = 31) and non-polyploid (maximum = 87, mean = 29, median = 22) clades, indeed, some of the more speciose polyploid clades were of higher taxonomic rank and so not present in the generic dataset (**Fig. 5.5**, panel F). Molluscs showed a similar pattern, with most of the polyploid clades removed having higher numbers of species than their non-polyploid sister clades (**Fig. 5.5**, panel H). In this case however, polyploid mollusc genera still had significantly more species than non-polyploid genera (V = 34, p-value = 0.023).

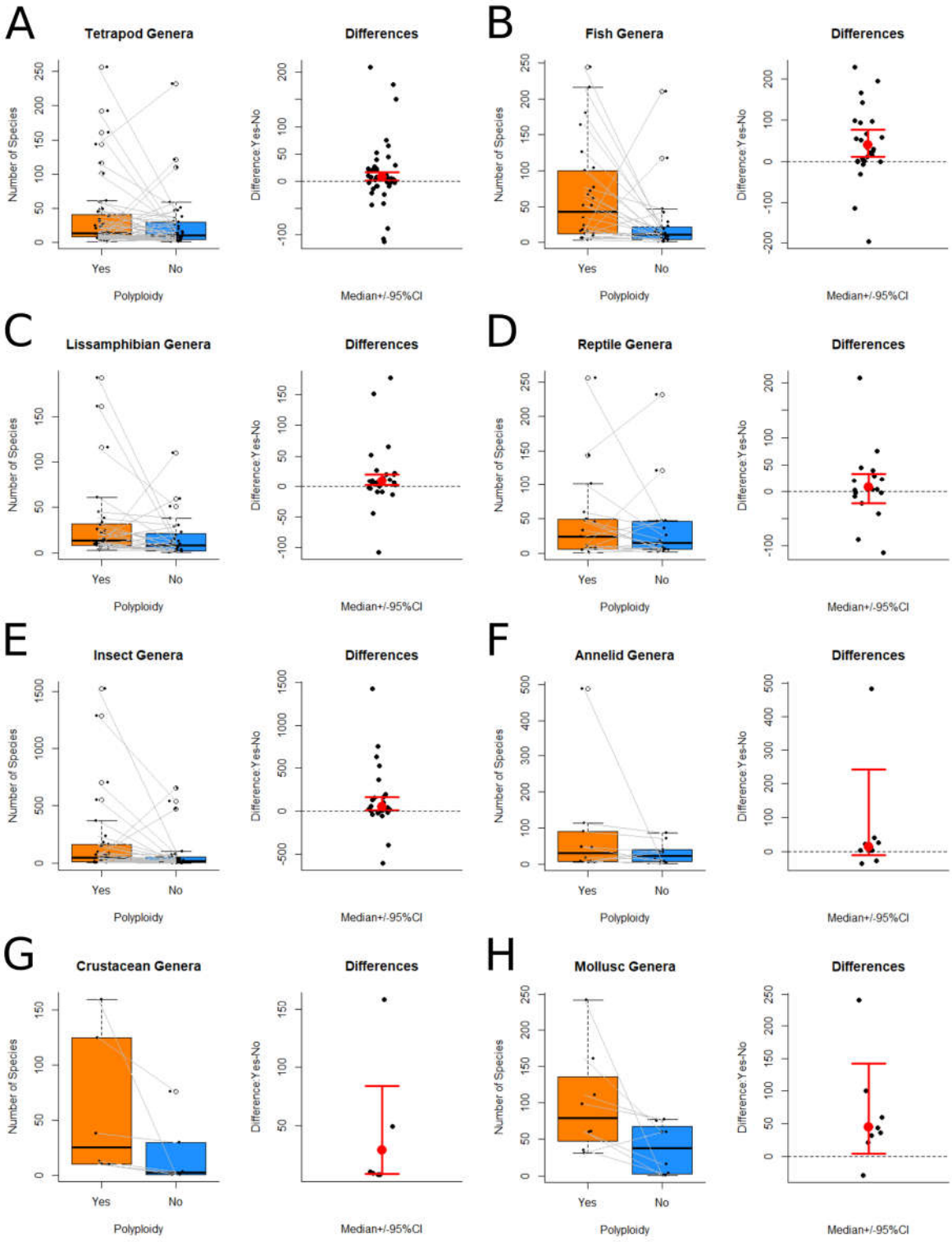

Fig. 5.5 Boxplots of raw values and differences in number of species between polyploid and non-polyploid genera in animal subgroups.

In the plant dataset, as the majority of clades were genera it is unsurprising that omitting higher ranked clades had very little impact on analyses. Within angiosperms, dicots (**Fig. 5.6**, panel A) showed significantly higher numbers of species in the polyploid clade sample (V = 2457.5, p-value = 0.003), while monocots (**Fig. 5.6**, panel B) did not (V = 251.5, p-value = 0.055). Gymnosperms (**Fig. 5.7**, panel A) and ferns (**Fig. 5.7**, panel B) produce identical results for the generic subsample (all clade pairs analysed in these two groups were genera).

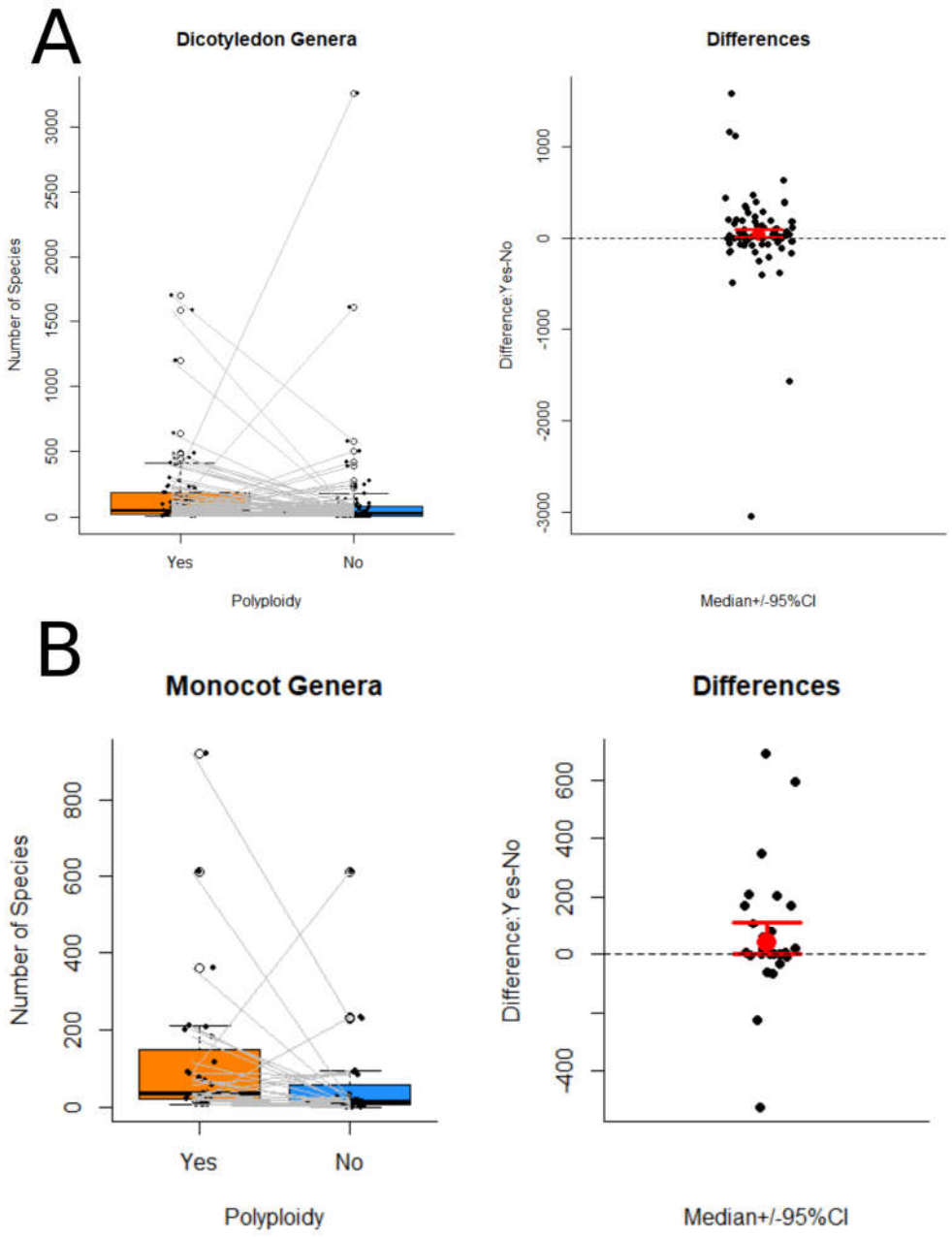

Fig. 5.6 Boxplots of raw values and differences in number of species between polyploid and non-polyploid genera in angiosperm subgroups.

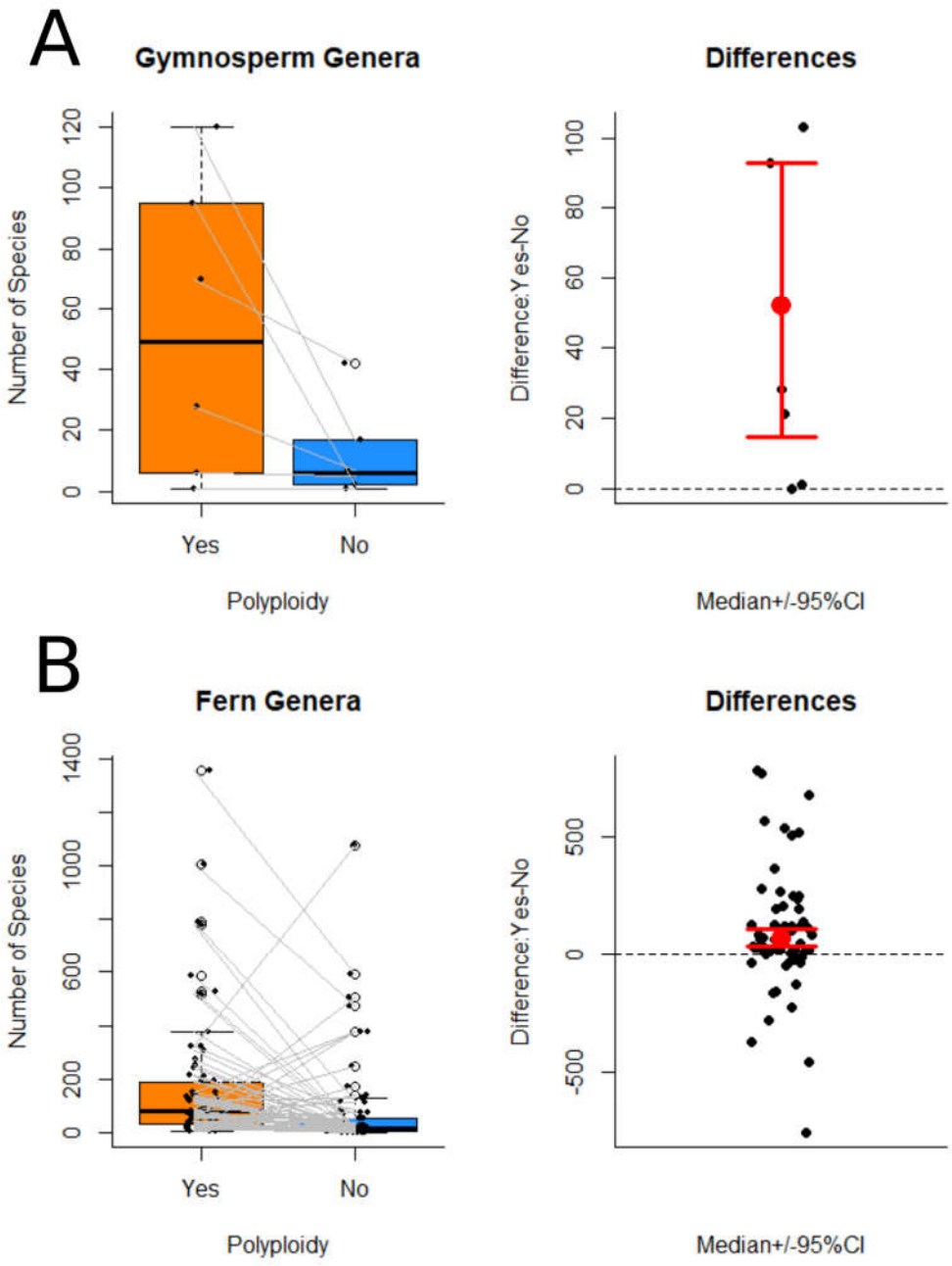

Fig. 5.7 Boxplots of raw values and differences in number of species between polyploid and non-polyploid genera in non-angiosperm subgroups.

5.3.3 Comparing The Diversity Of Polyploid & Non-polyploid Clades At Different Taxonomic Levels

Paired two-tailed Wilcoxon signed-rank tests on the data subsets revealed that the link between polyploidy and species diversity was present at a range of different taxonomic ranks (**Table 5.4**). Including clades of all taxonomic ranks was found to produce the most significant difference (V = 45769, p-value = 6.734×10^{-16}) between polyploid (maximum = 82,320, mean = 407, median = 52) and non-polyploid clades (maximum = 3,286, mean = 91, median = 15). Polyploid clades had a higher number of clades with very high numbers of species (**Fig. 5.8**, panel A) although a smaller number of non-polyploid clades were also found to have very high numbers of species. Although difference values were mostly clustered around the zero line close to the pseudo-median, positive differences were more numerous and of greater magnitude than negative differences (the highest positive differences were approximately twice the size of negative differences).

Despite being a much smaller dataset, clades above the rank of genus also showed a significant difference (polyploid: maximum = 82320, mean = 2952, median = 251, non-polyploid: maximum = 3286, mean = 289, median = 54, V = 493, p-value = 0.002). Although there were fewer outliers, the distribution of outliers was very similar to those of the whole dataset (**Fig. 5.8**, panel B). As with the whole dataset, polyploid clades at a rank above genus showed a greater range of values, particularly within the bounds of the upper and lower quartiles. The distribution of difference values was again similar to those for the whole dataset, although slightly less skewed towards positive values.

Dataset	Number of Clade Pairs	Wilcoxon signed-rank V	P-Value
All	356	45769	6.734×10^{-16}
Above Genus	35	493	0.002
Families	28	311	0.012
Subfamilies	4	7	0.626
Genera	321	36829	5.645×10^{-14}

Table 5.4 Paired two-tailed Wilcoxon signed-rank tests performed on polyploid and non-polyploid data subsets of different taxonomic ranks. **All:** the entire dataset of clades at all taxonomic ranks, **Above Genus:** all clades of a taxonomic rank above higher than genus.

Although there were insufficient pairs of orders and suborders to perform a robust statistical analysis (orders sample size = 2, suborders sample size = 1), families showed difference values that were even less skewed towards positive values than in the complete subset of clades above the level of genus (**Fig. 5.9**, panel A). This is primarily the result of polyploid and non-polyploid clades in the family level dataset having roughly equal numbers of outlier values with high numbers of species that were paired with low diversity clades in the other sample. Nevertheless, most of the species numbers in polyploid (maximum = 82320, mean = 3459, median = 251) clades were higher than the upper quartile of values for non-polyploid (maximum = 3286, mean = 322, median = 57) clades and as a whole polyploid clades showed significantly higher species counts than their non-polyploid sister clades (V = 311, p-value = 0.012). There were only 4 subfamily clade pairs, with no significant difference between polyploid and non-polyploid clades (V = 7, p-value = 0.626).

The lowest taxonomic rank analysed was genera and this subsample also constituted the majority of the clades in the dataset. Outlier values for the polyploid clades were generally higher than those of non-polyploid clades, although the number of species in a small number of non-polyploid clades equalled or exceeded the highest values seen in polyploids (**Fig. 5.9**, panel B). One non-polyploid clade in the generic dataset contained 3,257 species, as the polyploid genus *Bupleurum* is thought to be sister to a clade containing most of the genera in the celery family (Apiaceae). As a result, the non-polyploid clade in this case contained many diverse genera, resulting in an unusually high value. The rest of the clades tended to show positive difference values relative to the pseudo-median, with polyploid clades having significantly more species than non-polyploids (polyploid: maximum = 1697, mean = 129, median = 46, non-polyploid: maximum = 3257, mean = 70, median = 13, V = 36829, p-value = 5.645×10^{-14}).

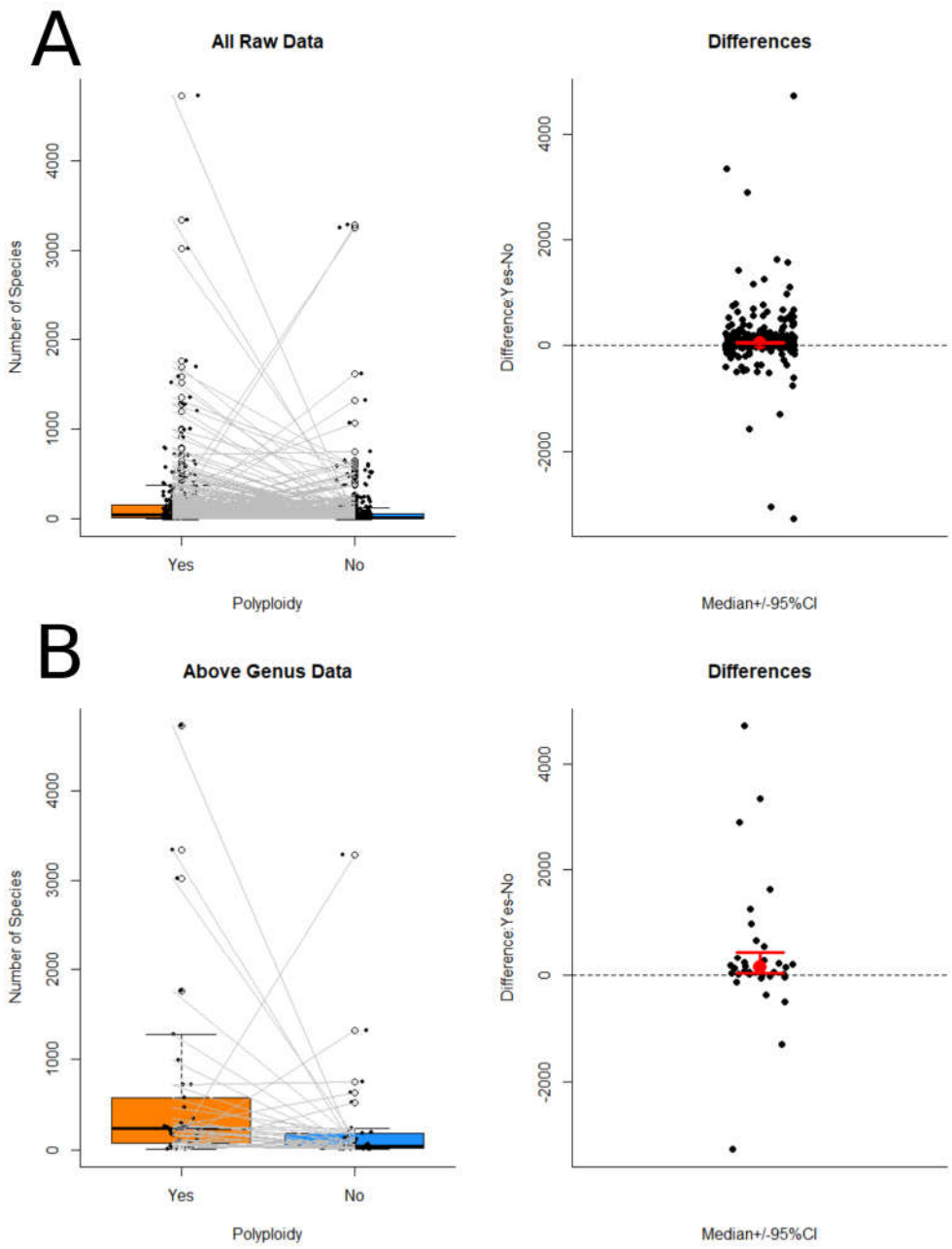

Fig. 5.8 Boxplots of raw values and differences in number of species between polyploid and non-polyploid clades in different subsets of taxonomic ranks. **A:** Differences between polyploid and non-polyploid clades across the entire combined dataset for all clades. **B:** Differences between polyploid and non-polyploid clades across the dataset of all clades above the rank of genus. Boxes delimit the upper and lower quartiles of the data, while central bars are median values. Whiskers delimit plus or minus 1.5 times the inter-quartile range, from the first and third quartiles. Grey lines connect pairs of values from the same clade. Differences given are values from polyploid minus non-polyploid clades, with positive differences indicating higher values in sample of polyploid clades. In the null case, difference values would be randomly distributed around the estimated pseudo-median shown in red, with upper and lower 95% confidence intervals.

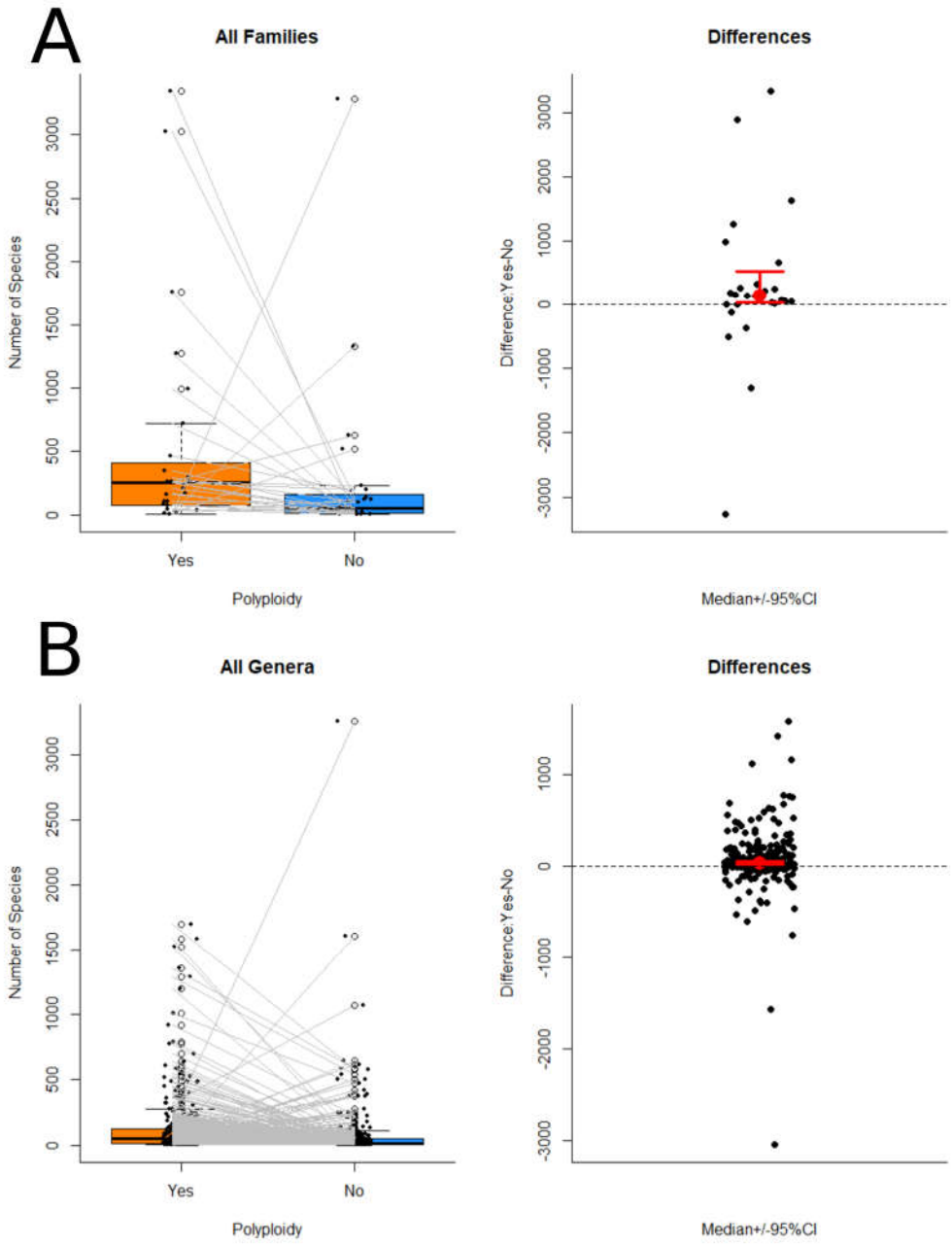

Fig. 5.9 Boxplots of raw values and differences in number of species between polyploid and non-polyploid clades at different taxonomic ranks. **A:** Differences between polyploid and non-polyploid families. **B:** Differences between polyploid and non-polyploid genera. Boxes delimit the upper and lower quartiles of the data, while central bars are median values. Whiskers delimit plus or minus 1.5 times the inter-quartile range, from the first and third quartiles. Grey lines connect pairs of values from the same clade. Differences given are values from polyploid minus non-polyploid clades, with positive differences indicating higher values in sample of polyploid clades. In the null case, difference values would be randomly distributed around the estimated pseudo-median shown in red, with upper and lower 95% confidence intervals.

5.4. Discussion

Clades where there is inferred to be a duplication of chromosomes (polyploidy) contain, on average, significantly more (p-value = 6.734×10^{-16}) species (mean = 406) than their non-polyploid sister clades (mean = 93). Therefore, the null hypothesis, that clades containing an increase in ploidy level do not have a greater number of species than sister clades which do not show an increase in ploidy level, is rejected. Polyploidy is far more frequent in many clades at lower taxonomic levels, with 90% of the comparisons in this dataset being between genera. Although polyploidy at higher levels does occur, the number of examples identified and included in the analyses was far lower: out of 356 clade pairs only 35 compared suprageneric clades. Clade pairs of a lower taxonomic rank are often nested within clade pairs of higher taxonomic rank, resulting in some of the data in the full analysis being non-independent. This does not seem to have biased the findings of this study however, as a separate analysis at the level of genera showed that genera inferred to be polyploid contain significantly more species than non-polyploid sister genera (p-value = 5.645×10^{-14}). Although small sample sizes did impact analyses in some cases, most of the major organismal groups studied showed a similar pattern regardless of how frequently polyploidy occurred. Similarly, although the dataset largely consisted of genera-level comparisons, the same pattern was found comparing clades of higher taxonomic rank separately and in a separate analysis of clades at the family level. These results suggest that far from being 'evolutionary dead ends' polyploid clades may have a stronger tendency to diversify and evolve new traits than other clades. While further investigation is required to determine what exactly drives these patterns, one of the most plausible explanations is that polyploidization introduces redundancy into the organism's genome, removing some generic constraint and allowing genes to develop novel functions.

5.4.1 Examples Of Polyploidy Are Most Prevalent In Flowering Plants, Fish, Amphibians & Insects

5.4.1.1 Distribution Of Polyploidy In Plants

Polyploidy was first identified in plants and has long been recognised as a prevalent and powerful evolutionary force within the group (Lutz 1907; Winge 1917; Stebbins 1950). Although many plant clades were recognised to have polyploid origins, whether polyploidy contributed significantly to evolutionary process was in doubt (Wagner 1970; Stebbins 1971). More recent studies in a wide range of plant clades have shown that polyploidy is not only extremely common, but that it has important evolutionary consequences (Barker, Husband, et al. 2016). While inconsistent patterns of evolution

in different polyploid plant clades have impeded the development of a 'unified theory of polyploidy' at least some of the outcomes of polyploidy are now becoming predictable (Soltis et al. 2016). The tendency plants show towards higher numbers of species in polyploid groups demonstrates a strong evolutionary pattern that might help to inform further studies of polyploidy in the group. Reviewing the literature also reveals that polyploidy is extremely prevalent within certain groups, such as derived angiosperms (monocots and eudicots) and pteridophytes (ferns) but much less common in gymnosperms (e.g. conifers and cycads) and basal angiosperms (e.g. Nymphaeales and Austrobaileyales). Several prior studies have stressed the link between polyploidy and speciation in angiosperms (Crepet and Niklas 2009), with most angiosperm clades inferred to have polyploid ancestry (Leitch and Bennett 1997; Soltis and Soltis 2004; Soltis and Soltis 2016). Ferns also constituted a large sample of our dataset, agreeing with earlier work that estimated that nearly half of the recent changes in haploid chromosome number occurred via polyploidy (Otto and Whitton 2000). Despite its high frequency, polyploidy in ferns has not been appreciated until recently (Schneider et al. 2017; Dauphin et al. 2018). As all of the fern clade pairs compared in this study were genera, the absence of polyploidy at higher taxonomic levels could be the reason the evolutionary consequences of polyploidy in ferns has received little interest. Unlike the situation in ferns, this study identified few documented instances of natural polyploids in basal angiosperms and gymnosperms. Polyploidy is famously rare in living gymnosperms (Ahuja 2005), although recent studies suggest ancient gene duplications may have occurred basally in major conifer clades (Li et al. 2015).

5.4.1.2 Distribution Of Polyploidy In Vertebrates

Numerous documented instances of polyploidy were also found in major animal groups, mainly within fish, amphibians and insects. The evolutionary importance of polyploidy in animals is much more contentious than in plants and has largely focused on ancient Whole Genome Duplication events (WGDs). Ancient polyploidization events are inferred to have occured twice in the ancestral vertebrate (Dehal and Boore 2005) and once somewhere basally in bony fish (Taylor et al. 2003), having been linked to bursts in the evolution of novel morphologies and more complex phenotypes (Burke et al. 1995). The inclusion of the fossil record generally reduces support for these hypotheses, however, leading some to argue there is little evidence genome duplications in these groups had long term evolutionary impact (Donoghue and Purnell 2005). Living examples of basal vertebrates and gnathostomes are incredibly rare with very long evolutionary branches separating them from other vertebrate groups, making it difficult to assess the impact of polyploidy in early vertebrates. At least two orders of ray-fined fish (Actinopterygii) are

thought to have arisen through polyploidy, the Acipenseriformes (e.g. sturgeons and paddlefish) and the speciose Salmoniformes (e.g. salmon, trout, gar) suggesting that polyploidisation events other than the ancient WGDs linked to *Hox* gene development have had a significant impact on vertebrate evolution. Polyploid families are also common within Siluriformes (catfish) and Cypriniformes (e.g. carp and minnows) and polyploid genera are found within most teleost groups. Previous authors have recognised the prevalence of gene duplications in teleosts especially (Braasch and Postlethwait 2012), where paralogues appear to often be conserved for developmentally important genes (Kassahn et al. 2009). At least some of these paralogues are associated with physiological traits which teleosts possess uniquely among vertebrates, such as their wide diversity of pigmentation types and colour patterns (Braasch et al. 2009). Polyploidy seems not to occur in the cartilaginous fish (Chondrichthyes) with rare exceptions such as the electric ray (Torpedo). Estimated substitution rates in cartilaginous fish are much lower than in tetrapods (Renz et al. 2013), while evolution of protein coding regions in teleosts are much faster (Ravi and Venkatesh 2008). Genetic constraints could therefore be much greater in chonricthyians, dramatically reducing the chances of reproductively viable polyploids from arising.

Within the rest of the vertebrates, the large majority of polyploid clades were amphibians, with some polyploids also documented in reptiles. Ploidy levels in these groups appear to be less evolutionarily conserved than in teleosts, with polyploid and non-polyploid taxa often being closely related. As a result, all but one of the clade pairs analysed were genera, although these clades were spread evenly across the major groups of lissamphibians and squamate reptiles. Although polyploidy has been recognised as common in particular groups of anurans, such as the clawed frogs (Evans et al. 2004) it has only been directly linked to speciation in a few specific cases (Ptacek et al. 1994; Martino and Sinsch 2002). This study demonstrates that documented cases of polyploidy in amphibians and reptiles, while not as frequent as in plants and teleosts are more common than previously appreciated. Even more surprising are the documented cases of polyploidy in birds and mammals, although these are far more tentative and controversial. While ZZW triploidy can occur in the domestic chicken (*Gallus gallus domesticus*) embryo mortality is extremely high (Clinton 1998). Triploidy also occurs in the Blue-and-Yellow Macaw (Tiersch et al. 1991). While polyploidy in birds is often associated with the expression of an intersex phenotype, the Blue-and-Yellow Macaw is a sexually monomorphic species and therefore polyploids seem to express the standard phenotype with no observable differences. Polyploidy is even less frequent in mammals, to the point where naturally occurring polyploids were seen as a practical impossibility. Nevertheless, the mountain viscacha rat shows numerous repetitive gene segments and has been punitively characterised as an allotetraploid with a hybrid origin (Suárez-Villota

et al. 2012), although its status as a true tetraploid remains questionable (Svartman et al. 2005; Evans et al. 2017).

5.4.1.3 Distribution Of Polyploidy In Invertebrates

Just over half of the documented polyploid invertebrate clades found for this study were insects (32 out of 62). This contrasts somewhat with previous estimates of polyploidy in the group; despite well over 2 million species, the number of polyploid insect clades is thought to be less than 100 (Lokki and Saura 1980). This discrepancy may be because sampling was dictated largely by the availability of published studies documenting polyploidy. While this is likely to affect sample composition and size for all of the clades investigated, it is particularly likely to affect the data analysed for invertebrates, because polyploidy in invertebrates has received relatively little study compared to vertebrates (Otto and Whitton 2000; C. Song et al. 2012). Previous studies of polyploidy focused largely on insects for several reasons. Firstly, the segmented bauplan of arthropods has been the focus of research on the role of *Hox* gene changes and duplications in determining the expression of morphological traits such as limb identity (Hughes and Kaufman 2002; Lemons and McGinnis 2006). Secondly, the fruit fly *Drosophila* is the most commonly studied model organism for studies of genetic evolution and expression in animals. Lastly, insects have extraordinarily high diversity and are major components of almost all terrestrial ecosystems despite having a relatively invariant bodyplan. Therefore, while the higher number of instances of polyploidy recorded in insects could be due to genuine differences in *Hox* gene expression allowing genetic changes to produce a greater variety of morphological forms (Galant and Carroll 2002; Ronshaugen et al. 2002), it could also simply be the result in biases in research effort towards studying these self-same mechanisms.

5.4.2 Polyploid Clades Contain Significantly More Species Than Non-Polyploid Clades

Polyploid clades were found to have significantly higher numbers of species than their non-polyploid sister clades (p-value = 6.734×10^{-16}), both across all clades and in most subgroups tested. This strongly implies polyploidy is an important evolutionary process which helps to facilitate diversification in many clades. Relatively few analyses of species diversity in polyploid and non-polyploid clades have been carried out (Petit and Thompson 1999; Otto and Whitton 2000), and only one of these accounted for differences in clade size as a result of age (Vamosi and Dickinson 2006) and all have focused exclusively on plants. Some authors have argued that, despite being relatively rare, WGDs have had a profound impact on diversification in cases where specific

conditions have allowed polyploids to persist (Van De Peer et al. 2009). Early attempts to explain the abundant occurrence of functional plant polyploids proposed that genome doubling could restore chromosome pairing in otherwise infertile hybrids (Winge 1917). Although polyploidy is now recognised as extremely common in certain groups, several authors have presented evidence that polyploid taxa show higher extinction rates and slower diversification rates than diploid groups and therefore represent 'evolutionary dead ends' (Mayrose et al. 2011; Arrigo and Barker 2012). The significantly higher diversity of polyploids, not only in angiosperms but in many other groups of plants and animals, suggests this is untrue: either polyploid clades have slower diversification rates but longer evolutionary histories on average (which is unlikely) or polyploids diversify more rapidly than their non-polyploid sister taxa. Although most polyploid populations are likely to go extinct over very short time periods (Rieseberg and Willis 2007; Soltis et al. 2010), higher extinction rates in persistent polyploid clades were not supported by subsequent analyses (Soltis et al. 2014). Although one could argue that some of the clades investigated in these analyses do not represent independent tests (due to the nesting of clades of different taxonomic levels) statistical analyses performed on pairs of genera only produced highly similar results.

There are several mechanisms by which polyploidy could promote speciation but, again, most specific investigations into these have focused on plant groups. Studies of transposable element (TE) evolution in the allopolyploid *Capsella bursa-pastoris* suggest that polyploid genomes in plants are subject to relaxed selection after a ploidal increase, effects that are likely to impact the genome for millions of years (Ågren et al. 2016). Polyploidization has also been linked to changes in sexual systems in plants (Ashman et al. 2013), and specifically sexual dimorphism in angiosperms (Glick et al. 2016). It has also been suggested that polyploidization could drive ecological change in angiosperms through changing pollinator, herbivore and pathogen interactions (Segraves and Anneberg 2016). The proportion of taxa exhibiting polyploidy appears to be higher in glaciated regions, where there is frequent contact between previously isolated populations. In these circumstances, the fact that different ecological traits from two parent species could be fixed and combined heterozygously in polyploid hybrids may confer a selective advantage (Leitch and Bennett 2004).

While polyploidy is traditionally seen as rare or unimportant in animals (Mable et al. 2004) this study shows higher diversity in polyploid groups is clearly also present in many animal groups, suggesting that many of the mechanisms evident in case studies of plants may also occur in animals. Allopolyploidy resulting from hybridization could facilitate diversification by promoting increased physiological activity of certain traits (Heterosis). Heterosis is known to occur in animals and is an important factor contributing towards

the growth of domestic cattle (Macneil et al. 2017). Polyploidy also increases gene redundancy which could protect against iterative deleterious mutations and genotoxicity, particularly in populations that undergo severe bottlenecks (Comai 2005). Perhaps most importantly gene redundancy allows duplicate copies to partition complex functions and become more specialised (subfunctionalisation) or take on entirely new functions (neofunctionalization), facilitating the evolution of novel traits as well as greater specialisation and complexity (Moore and Purugganan 2005). It has also been proposed that polyploidy makes the evolution of self-compatibility easier, allowing many polyploids to develop modes of asexual reproduction (Barringer 2007).

The majority of plant and animal groups analysed showed higher diversity in polyploid clades, even when there were relatively few documented cases. In most groups, these differences were also highly significant (<0.001). Reptiles, annelid worms and magnoliids appeared not to fit this pattern. While the monocot and gymnosperm samples were also non-significant, both of these groups had relatively modest sample sizes and far lower p-values. While polyploidy in gymnosperms has been recognised as rare relative to angiosperms (Grant 1981), polyploidy is common in monocots (Goldblatt 1980). It, therefore, seems likely that at least the latter group may show a significant difference with the analysis of a larger sample of clades. Magnoliids probably also showed a non-significant result due to a small sample size, although previous studies have shown that polyploidy is extremely common within the group, at least in *Magnolia* (Rothleutner et al. 2010). In this case small sample sizes may have arisen from the need to find clearly defined polyploid and non-polyploid sister clades, rather than a difficulty in identifying polyploid taxa *per se*. In annelids, previous work in oligochaetes has suggested little correlation between genome size and life history traits, with the possible exception of parthenogenesis in highly polyploid earthworms (Gregory and Hebert 2002). Unlike magnoliids, polyploidy may be rare in annelids with the exception of some highly polyploid genera (Marotta et al. 2014) but it is difficult to be certain as there have been no comprehensive assessments of polyploidy in the group. The lack of an observed difference in reptile diversity is interesting considering that polyploidy in squamates has been relatively well studied, particularly with regards to the acquisition of parthenogenesis. There are no known examples of polyploidy or parthenogenesis in crocodilians or turtles. All but one of the naturally occurring cases are associated with hybridization and around 40% of parthenogenetic species are polyploid (Kearney et al. 2009). It could be that polyploid reptiles tend to evolve in environments less well suited to squamate diversification. Proportions of parthenogenetic squamate species appear to be higher in glacial environments where diversity is low; a study of *Heteronotia* showed that the distribution of parthenogenetic populations appears to be biased towards higher latitudes than their sexually reproducing ancestors (Kearney et al. 2003). Although

polyploidy is strongly linked to parthenogenesis, diploid parthenogenetic lineages do exist. Furthermore, viable polyploids only seem to occur as triploids (S. Song et al. 2012), likely arising through the mating of diploid hybrids with sexual lineages (Parker and Selander 1976). These factors could explain why both polyploidy and parthenogenesis are highly labile traits in squamates. There is also little support for strong ecological (Case 1990) or phenotypic differences (Cullum 2000) between parthenogenetic triploids and sexual diploids, which could help account for the lack of differences in diversity seen here.

5.4.3 Polyploid Clades Contain Significantly More Species Regardless Of Taxonomic Level

Polyploid clades also showed significantly greater diversity at higher taxonomic levels, making it unlikely that the recovered results are biased by the scale at which clades are sampled. However, documented cases of polyploid genera do seem to be far more common (321 out of 356 clade pairs) than for higher taxonomic levels. As closely related taxa are more genetically similar it would make sense that polyploidy might arise convergently many times in closely related taxa within the same clade. Ultimately, polyploidy must first arise as small populations within a species before possibly persisting over longer periods of evolutionary time. While polyploidy is very common in certain groups of animals and particularly plants, most polyploids probably go extinct quickly (Ramsey and Schemske 1998), making it much less likely to persist in larger clades. Instead, it is a few highly successful polyploid lineages which persist and diversify greatly seem to account for a dissproportionate amount of taxonomic diversity. Even if a large clade does have a polyploid origin it will very likely be difficult to detect as the genetic signal of the ploidy event is overwritten by subsequent loss of non-functioning genes, mutation in retained genes and even subsequent ploidy events (Blanc et al. 2003). A number of biological factors, therefore, make it likely that ploidy events are most common at lower taxonomic levels but also exaggerate this pattern by hampering our ability to detect it in large clades.

Most attempts to survey polyploidy to date have dealt mainly with documenting its occurrence at these low taxonomic levels (Gregory and Mable 2005; Wood et al. 2009), while discussions of its evolutionary significance in the long term have focused on ancient Whole Genome Duplications (Mable et al. 2011; Soltis and Soltis 2016). The fact that differences in polyploid and non-polyploid diversity hold true for clades of all sizes and taxonomic ranks of all sizes implies that many evolutionarily important instances of polyploidy are likely being missed by focusing on these two extremes. While previous studies have identified families and subfamilies with polyploid origins in flowering plants (Schranz and Mitchell-Olds 2006) and fish (Šlechtová et al. 2006), the evolutionary

importance of polyploidy in clades of this size has seen little discussion. The significant difference in diversity of polyploid and non-polyploid clades at the family level suggests that ploidy events are likely important promotors of phenotypic diversity over longer evolutionary timescales than initially thought.

5.4.4 Conclusions and Further Study

In this chapter, analyses conducted on 712 animal and plant clades find that polyploid clades contained significantly more species that non-polyploid clades, even when fossil taxa are included. This result holds at both the family and genus levels and across a wide range of plant and animal groups. Some statistical analyses, particularly for invertebrate groups and higher taxonomic levels are limited by small sample sizes. Polyploidy has historically seen as both more prevalent and evolutionarily more important in plants (Mable et al. 2004), particularly in angiosperms, and rare or unimportant in animals. Although polyploidy is now being identified in an increasing number of vertebrate groups, principally in teleosts (Braasch and Postlethwait 2012) and some anurans (Ptacek et al. 1994), these biases have left polyploid groups such as ferns, many amphibian groups and invertebrates very much understudied. Comprehensive assessments of polyploidy in undersampled groups is needed to determine whether polyploidy is genuinely less common in some clades. Secondly, it would help to confirm the generality of the patterns observered here.

Regardless of small sample sizes in some poorly studied groups, the widespread and highly significant differences in species diversity recorded here represent a compelling case for genome duplication and polyploidy facilitating diversification in many groups of organisms. These findings support the hypothesis that most organisms are subject to strong genetic constraints (Arnold 1992) and that these constraints are an important cause of convergent evolution (Stern 2013).

6 Final Conclusions And Future Work

Convergent evolution, the independent acquisition of the same novel traits in unrelated lineages, suggests evolution is constrained to particular outcomes. This contrasts with traditional views of evolution as an open-ended process and has led some to propose that evolutionary process might be, to some extent, predictable. Convergent evolution manifests in a number of macroevolutionary patterns. Only through quantitative methods can a complete understanding of the nature of these patterns and how they are produced be reached. This thesis aimed to develop understanding of the macroevolutionary impacts of convergent evolution over geological timescales and across major groups. It built on current evolutionary understanding of convergent evolution in a number of novel ways. Firstly, it compares macroevolutionary patterns across the tree of life, in order to test whether major groups of animals and plants evolve according to a predictable template over geological timescales. Secondly, it investigates the utility of biogeography in identifying cases of convergent evolution and testing competing phylogenetic hypotheses. Thirdly, it tests the possible role of genome duplication events in removing genetic constraint and facilitating diversification.

6.1 Main Conclusions

This thesis yielded the following key findings:

1) Plant clades, like those of animals, show early high disparity, with an initial phase of evolution during which most regions of their morphospace are colonized and levels of overall disparity approach or attain maximum levels. Centre of gravity (CG) values for the disparity profiles of most plant clades assessed were bottom heavy (CG < 0.5). While angiosperms and ferns showed remarkably constant disparity through time, conifers expand incrementally as specific sub-clades radiate. The similarities in disparity patterns across both plants and animals suggests that common mechanisms constrain evolution and promote convergence across the tree of life.

2) Most clades of animals show evidence of character exhaustion, with a slowdown in the rate at which novel characters appear laterin their evolutionary history. In a sample of 93 extinct major clades, groups realised an average of 60% of their inferred

maximum numbers of states, but all continued to evolve new states up until their extinction. Despite this, there were no significant relationships between any indices of exhaustion curve shape and the clade disparity CG. Clades showing early high-disparity were no more likely to have early character saturation than those with maximum disparity late in their evolution. The limited overall disparity of clades can, therefore, not be explained purely by the rate at which novel characters evolve. Instead, limited availability of niches, competitive exclusion or intrinsic biological constraints must impose limits on the range of form that organisms can evolve.

3) In a sample of 48 plant and animal clades with relatively well known biogeography, geographical distributions were found to be more consistent with molecular phylogenies than morphological topologies in around 70% of cases, despite no significant difference in the years the trees were published (Wilcoxon p-value = 0.362). Although different measures of phylogenetic fit gave somewhat different results most indicate a significant difference. Biogeographic HER is proposed to give the most accurate measure of biogeographic congruence and yielded the most significant difference (Wilcoxon p-value = 0.002). A significant difference was found in the number of characters making up morphological and molecular datasets (Wilcoxon p-value = <0.001), supporting the assertion that molecular phylogenies are more reliable in part because they are based on analysis of a greater number of characters. Comparison of stratigraphic and biogeographic congruence in a smaller sample of clades was inconclusive, with both stratigraphic and biogeographic measures only favouring molecular trees in 30-40% of cases. While further tests would be needed to evaluate different measures, these results support the use of both stratigraphic and biogeographic data as complimentary tests of phylogeny and suggest that many examples of convergent evolution arise in environments subject to similar ecological and adaptive pressures.

4) Clades in which genome duplications occurred showed significantly higher diversity than their non-polyploid sister clades (Wilcoxon p-value <0.001), based on a comparison of the number of species in 356 pairs of clades of animals and plants. The same differences were also recovered in nearly all major groups of vertebrates, invertebrates and plants in which polyploidy has been documented, suggestive of the importance of polyploidy in driving diversification not only in flowering plants but also insects and some vertebrate clades. These results support the hypothesis that duplication events act to remove genetic and developmental constraints by increasing redundancy and weakening or removing pleiotropic effects and indicate that such constraints significantly limit evolutionary potential in many different groups.

6.2 Convergence Shapes Macroevolution Over Geological Time, But The Mechanisms Are Likely Situational

Traditional views of evolution see the possible variation in organisms as largely open-ended, with novel morphologies evolved adaptively in response to natural selection (Darwin 1859; Lull 1906; Elmer and Meyer 2011). Over long time scales, chance events and environmental change have a marked impact on both the selective pressures organisms are subject to and which lineages persist through time (Rees 2002; Jablonski 2005; Ruta et al. 2011) in a highly contingent fashion (Gould 1989). This model of evolution is highly chaotic to the point of being unpredictable, as each state is influenced by prior random events. Several authors since then have compellingly argued that the exact opposite is true, that in actuality evolution is constrained to develop a finite number of outcomes and that morphological forms are both limited and predictable (Conway Morris 2010; McGhee 2011).

The main contention of this thesis is that identifying which of these two pictures of evolutionary process is most correct requires empirical evaluation of general evolutionary patterns, not in one group of organisms but in many. It is only by comparing across as inclusive a sample as possible that the generalities of evolutionary process and specifically convergence will be revealed. While many authors have discussed the importance of convergent evolution in specific clades (Mares 1993; Conway Morris 1998; Conway Morris et al. 2008; Gheerbran et al. 2016), there is a growing movement to quantify and empirically assess convergence directly (Stayton 2006; Stayton 2008; Ingram and Mahler 2013; Arbuckle et al. 2014). However, these studies have not attempted to look at how convergent evolution influences general evolutionary patterns across *all* groups. Most specific measures of convergence (Stayton 2015) are not well suited to this task, because they either require a large amount of prior information which is not easily obtainable, or can only be employed to investigate convergence across groups with similar forms (Chapter 1).

One solution is to investigate patterns of overall disparity using non-specific measures of similarity and difference, such as the discrete character states of cladistic matrices (Wills et al. 1994; Ruta and Wills 2016). This method also has the advantage of utilising the considerable wealth of existing morphological data used to infer evolutionary relationships to directly study the evolution of form. Previous work used this approach to assess general disparity patterns across a wide range of clades and found evidence that overall disparity was restricted, with most clades reaching high disparity early in their evolutionary history (Hughes et al. 2013). Analysis of disparity patterns in major groups of vascular plants (Chapter 2) showed that despite fundamental structural and physiological differences (Farnsworth and Niklas 1995; Adams and Wendel 2005;

Barthélémy and Caraglio 2007) plants also show evidence of overall disparity being restricted. This strongly implies that there are generalities to evolutionary process and that similar mechanisms are shaping disparity patterns in these two highly disparate groups. However, there are also notable differences. While the disparity of most plant clades analysed was relatively constant, conifer disparity showed evidence of incremental increases in disparity over the first half of their evolutionary history as new sub clades appear. While overall disparity patterns show broad similarity, patterns of morphospace occupation differ between clades. For example, leptosporangiate ferns and pines show evidence of diversifying successively into new areas of the morphospace, while angiosperms seem to have explored the range over overall morphologies early in their evolutionary history, with new subclades occupying intermediate morphologies between previous groups. For these generalities to be confirmed it would be useful to carry out a more comprehensive study of disparity in plants across as broad a spectrum of angiosperm, gymnosperm and pteridophyte groups in order to develop a more complete understanding of how the processes creating novelty and constraint differ across the major groups of macroscopic life, although in practice this would likely require the formulation of coding of new matrices from herbarium collections for many groups. While discrete morphospace approaches are powerful in that they allow disparity patterns to be compared across a wide range of morphologically disparate clades, they provide limited insight into the details of morphological variation and change. Such studies are well complemented by more typical landmark and semi-landmark based analyses (Goswami et al. 2011; Chartier et al. 2014) of specific clades, features and time periods of interest to gain a more detailed understanding of the processes giving rise to overall disparity patterns.

The ubiquity of early high disparity patterns is strongly suggestive of a similarly ubiquitous driving mechanism. The most likely candidate seemed to be the tendency for clades to exhibit slowdown in the rate at which they evolve novel characters (Wagner 2000). As one proceeds from the root to the tips of a phylogeny a greater proportion of the number of morphological character state changes are characters which have already evolved earlier on that branch or elsewhere in the tree. This phenomenon of character exhaustion has been recognised in many clades and is a plausible explanation for the observed patterns of early high disparity. It is, therefore, surprising that there is no evidence at all of a clear link between the rate of character exhaustion and the shape of the clade's disparity profile (Chapter 3). Clades reaching maximum disparity late in their evolutionary history were just as likely to show high levels of character exhaustion than clades with early high disparity. Studying the morphospace occupation of clades through time gives a possible explanation, as clades with similar disparity profiles can differ greatly in how they colonise morphospace. While some clades occupy a similarly sized

area of the morphospace, the position of that envelope may move through time (Wills 1998a; Wills et al. 2012). Other clades quickly colonise extremes to create a large morphospace envelope but subsequently sub-divide this envelope evolving new states in morphologically 'intermediate' taxa (Gerber 2011). In both of these cases new character states continue to evolve (new areas of the morphospace are colonised) but overall disparity remains constant.

The weak correlation negative correlation found between total levels of homoplasy (indicated by the HER) and disparity (indicated by profile CG) suggests that overall disparity is limited by the amount of convergence and reversal in the clade, but that neither of these properties correspond to the rate of novel character evolution. The decoupling of overall disparity patterns and character exhaustion is also strongly suggestive of differing rates of character change in organisms, with some characters becoming 'fixed' early in evolution and others continuing to vary and evolve novel states even until extinction. As evolution proceeds, characters associated with general body-plan (Bauplan) are likely to become canalised and invariant (Peterson et al. 2009; Goswami and Polly 2010), acting as a template upon which further variation and character state iteration occurs. The kinds of discrete character morphospaces and cladistic exhaustion analyses used in these kinds of studies fail to distinguish between characters of different developmental levels or depths. Complementary morphometric approaches are being developed (Brakefield 2008; Mitteroecker and Huttegger 2009; Gerber et al. 2011) which would likely facilitate these kinds of investigations. The methods for generating character exhaustion profiles are also simplifications of actual evolutionary process. Firstly, the phylogenies used relative ages to order the nodes rather than actual time calibrations. Therefore the 'rates' of exhaustion are abstractions rather that representing any kind of genuine evolutionary rate. Scaling the distance between all points in the curve by the length of branches on a fully time calibrated tree would solve this problem but would also be time consuming and reliant on accurate dating of nodes and tips. For this reason, relatively vague properties of curve shape were used rather than more exact measures. Better models of character state change could also be used to more accurately fit curves to character exhaustion profiles also, although this would likely require some assumptions regarding evolutionary process. Iterative methods of curve fitting could also be applied, but in this case it is somewhat unclear what the coefficients would represent in biological terms.

While restrictions on the evolution of morphological disparity do not appear to be driven directly by the rate at which new characters evolve in clades, there are other mechanisms that could also limit the range of possible evolvable forms and so drive patterns of convergence. These can broadly be divided into two categories, extrinsic ecological

constraints and intrinsic genetic or developmental constraints. Evidence of ecological controls on disparity come from adaptive radiations, where clades explosively diversify to take advantage of new environments, either in the wake of mass extinctions (removal of competitors) (Toljagic and Butler 2013; Halliday et al. 2016) or with range expansions and the colonisation of new geographical areas (expansion of ecospace or opening of new niches) (Pinto et al. 2008; Muschick et al. 2012). Many adaptive radiations show evidence of convergent evolution towards similar bodyforms, ecologies, or both. Well known examples include radiations of cichlid fish in African Rift Valley lakes (Muschick et al. 2012), island radiations of *Anolis* in the Greater Antilles (Mahler et al. 2013) and the convergent evolution of similar forms in marsupial and placental mammals (Goswami et al. 2011). In some cases convergent evolution appears to have obfuscated phylogenetic relationships (Gaubert et al. 2005). For example, molecular constructions of placental mammal phylogeny support a number of largely endemic clades, in stark contrast to traditional views of mammalian phylogeny (Asher et al. 2009; O'Leary et al. 2013; Tarver et al. 2016).

This pattern is not unique to mammals, in a sample of 48 clades of animals and plants the distributions of extant taxa were significantly more congruent in 60-71% of cases (Chapter 4). Congruence values, particularly those of Biogeographic HER, were shown to increase very slightly with both the number of phylogenetic characters the tree was based on and the publication year, consistent with phylogenetic estimates improving both over time and with the analysis of larger matrices. While there was no significant difference in the publication dates of morphological and molecular trees there was a highly significant difference in the number of phylogenetic characters. This agrees with current consensus; the reliability of phylogenetic inference improves with the inclusion of more characters (Hillis et al. 2003; Rokas and Carroll 2005). Comparisons of stratigraphic and biogeographic congruence measures were limited by a small sample size but suggest that biogeographic measures are about as good a test of phylogenetic hypotheses as stratigraphy. Carrying out a separate study specifically designed to evaluate different measures of biogeographic and stratigraphic congruence in more detail would be valuable but would likely be limited to a few study clades with exceptionally well characterised fossil records and distributions. The biogeographic tests employed here were relatively simple in that they only examined the present distributions of extant taxa. Palaeodistributional data from fossils could be incorporated in several ways. The simplest way would be to use the fossil data to infer centres of origin for living taxa, as taxa may have originated in a different biogeographic region and changed their distributions as a result of range expansions and local extinctions. Alternatively, a more thorough approach assessing congruence at different time slices up a phylogeny could be used. More advanced methods could, of course ,be implemented using model

inference (e.g. the DEC model) in software such as RASP or the R package BioGeoBears (Matzke 2014; Yu et al. 2015). The main reason these approaches were not adopted in this study, besides the lack of suitable priors for the *e* (extinction), *d* (dispersal) and *j* (founder event speciation) variables, is that it introduces circularity of inference. Biogeographic models infer the most probable biogeographic history given a phylogeny, therefore the biogeographic histories inferred are dependent on the phylogeny used. One could also incorporate biogeographic data directly into phylogenetic analyses in a manner similar to traditional historical biogeography analyses (Nelson and Platnick 1981; Morrone and Crisci 1995) but this would nullify the main advantage of using biogeographic data in the first place; namely that its value as an independent test to evaluate phylogeny.

Intrinsic genetic or developmental constraints also likely play a role in restricting disparity and promoting convergent evolution or parallelism as increasing pleiotropy and functional linkage makes it difficult to modify developmental programs (Anderson and Roopnarine 2005; Goswami and Polly 2010). One example is the highly conserved 7 cervical vertebrae of most mammals. While other groups of vertebrates seem able to modify this number through homeotic frameshifts (Burke et al. 1995; Sachs et al. 2013), such shifts in mammals are associated with a number of problems, including elevated risk of juvenile cancer (Galis 1999). While sloths and manatees are able to vary this number, this is likely due to a lower metabolic rate making them more tolerant to the deleterious effects (Galis and Metz 2007; Varela-Lasheras et al. 2011). If these kinds of evolutionary constraints are common, we should see an effect in the evolution of clades in which these constraints are weakened or removed. One of the most common instances where this is likely to occur is in polyploid taxa, as duplication of the genome increases genetic redundancy. Greater levels of redundancy reduces the chance of a mutation leading to a deleterious pleiotropic effect. Polyploid clades do indeed show higher diversity than their non-polyploid sister clades in nearly all major groups in which polyploids occur (Chapter 5), at all taxonomic levels. While number of species was chosen for comparison in this study in order to facilitate as many comparisons as possible, future studies could test for differences in the disparity of polyploid and non-polyploid clades specifically, possibly including data from other groups also such as fungi (Albertin and Marullo 2012).

6.3 Ecological & Genetic Constraints Likely Shape Evolution, But Further Studies Are Needed

Taken together, the findings of this thesis suggest that convergent evolution is prevalent enough to manifest at the macroevolutionary scale in patterns of disparity, character evolution and diversification. Such patterns are likely driven by some combination of extrinsic (ecological) and intrinsic (genetic or developmental) constraints, suggesting a number of possible further lines of research.

6.3.1 Ecological Constraint

There are three types of natural experiment which would allow us to test the effects of removing ecological constraint

1. Mass extinctions, defined as events leading to the demise of 75% of species or more globally (Hallam and Wignall 1997), represent a rare opportunity to study how clades evolve in perturbed environments in which competition for niches has been greatly reduced or removed. Notable examples include the diversification of eutherian mammals (Halliday and Goswami 2016; Halliday et al. 2016) and teleost fish (Friedman 2010) in the wake of the K-Pg mass extinction. If ecological constraints are released after such events, fossil and extant clades which passed through extinction events during their evolutionary history (e.g. ammonoids, mammals, bivalves) should show increases in disparity which are significantly different from the expected range of values shown by clades radiating at other times (Hughes et al. 2013).

2. Instances of habitat transition, often precipitated by the evolution of key innovations allow organisms to radiate into fundamentally new environments and might facilitate increases in disparity. Particular examples of interest include the multiple transitions of terrestrial vertebrates back into marine settings (e.g. whales, sea cows and ichthyosaurs) (Kelley and Pyenson 2015) and the three instances of the evolution of vertebrate flight (birds, bats and pterosaurs) (Norberg 2012).

3. The strength of competitive interactions can also be tested indirectly by using a census approach (Benton 1996). Direct evidence of competition in the fossil record is scarce (Prada et al. 2016; Silvestro et al. 2016), but it is possible to test for asymmetries of interaction between clades. Where the origination of one

lineage is broadly coincident with the extinction of another, there is the possibility that the second lineage was competitively replaced by the first (but not vice versa). Such candidate competitive replacements (CCRs) can be further constrained using data that classifies lineages into broad ecological and palaeobiogeographical categories. Of particular interest would be the comparative strength of CCRs within clades radiating into vacated ecopace versus those not, and the interaction between sister clades with and without WGDs.

6.3.2 Genetic Constraint

The role of genetic constraints on evolution can be investigated through study of gene duplications at the large and small scale in a number of ways.

1. Whole Genome Duplications represent the most extreme circumstances under which pleiotropic constraints might be released. WGDs are known in vertebrates (Dehal and Boore 2005; Donoghue and Purnell 2005) and particularly common in many clades of flowering plants (Van De Peer et al. 2009; Soltis and Soltis 2016). Notable examples include the grasses, crucifers and legumes in addition to major clades such as monocots and rosids. In addition, most recent polyploid clades identified in this thesis have never been subject to empirical disparity analyses. If intrinsic constraints constrain disparity in a meaningful way, clades with basal WGDs should show higher initial disparity than clades lacking such events.

2. Small Scale Duplication of genes (SSDs) are widespread and common in nearly all clades (Taylor and Raes 2005), including clades where WGDs are rare (such as mammals) . The lack of empirical studies on SSDs is mainly a function of the difficulty of quantifying these more minor duplication events. However, for extant clades with annotated genomes, it is now possible to summarise changes in gene family size (GFS) and map this metric onto time calibrated phylogenies to see whether the position and magnitude of these changes correlates which the rate at which new species evolve (speciation rate) or the rate at which traits evolve (character state changes). If SSDs play a significant role in morphological evolution, we would expect branches with more inferred duplications to have higher speciation rates and higher rates of morphological trait evolution.

3. Many vertebrate groups prone to gene duplication (e.g. bony fish and amphibians) also seem to show highly complex and variable skeletal morphology,

but a link between the two has yet to be tested empirically. Arthropods and flowering plants provide us with further examples of groups prone to gene duplication, with body plans controlled by homeotic genes (Weigel and Meyerowitz 1994; Burke et al. 1995; Ronshaugen et al. 2002). In these groups, measures of the differentiation and number of different types per segment provide a simple metric of complexity. Clades with basal WGDs might be expected to show greater levels of complexity than sister clades lacking duplications. SSDs might also be expected to correlate with complexity measures when mapped onto phylogenetic trees.

6.4 Final Conclusion

Convergent evolution, the independent origination of novel traits in distantly related organisms, is one of the most striking and widespread signatures across the Tree of Life. While most studies of convergence have extensively documented and characterised convergence, empirical tests of the general patterns of convergence offer unique perspectives. Convergent evolution manifests at the macro scale as a limitation on the range of forms organisms can evolve and a reduced potential to evolve new characteristics. While convergence introduces phylogenetic noise into a significant number of trees based on morphological data, many examples of convergence have a biogeographic signal, a fact which might allow us to identify instances of convergence using distributional data. Mechanisms of extrinsic ecological constraints and intrinsic genetic constraint are implicated in many convergent evolutionary patterns and are, perhaps, more widespread than previously supposed.

7 References

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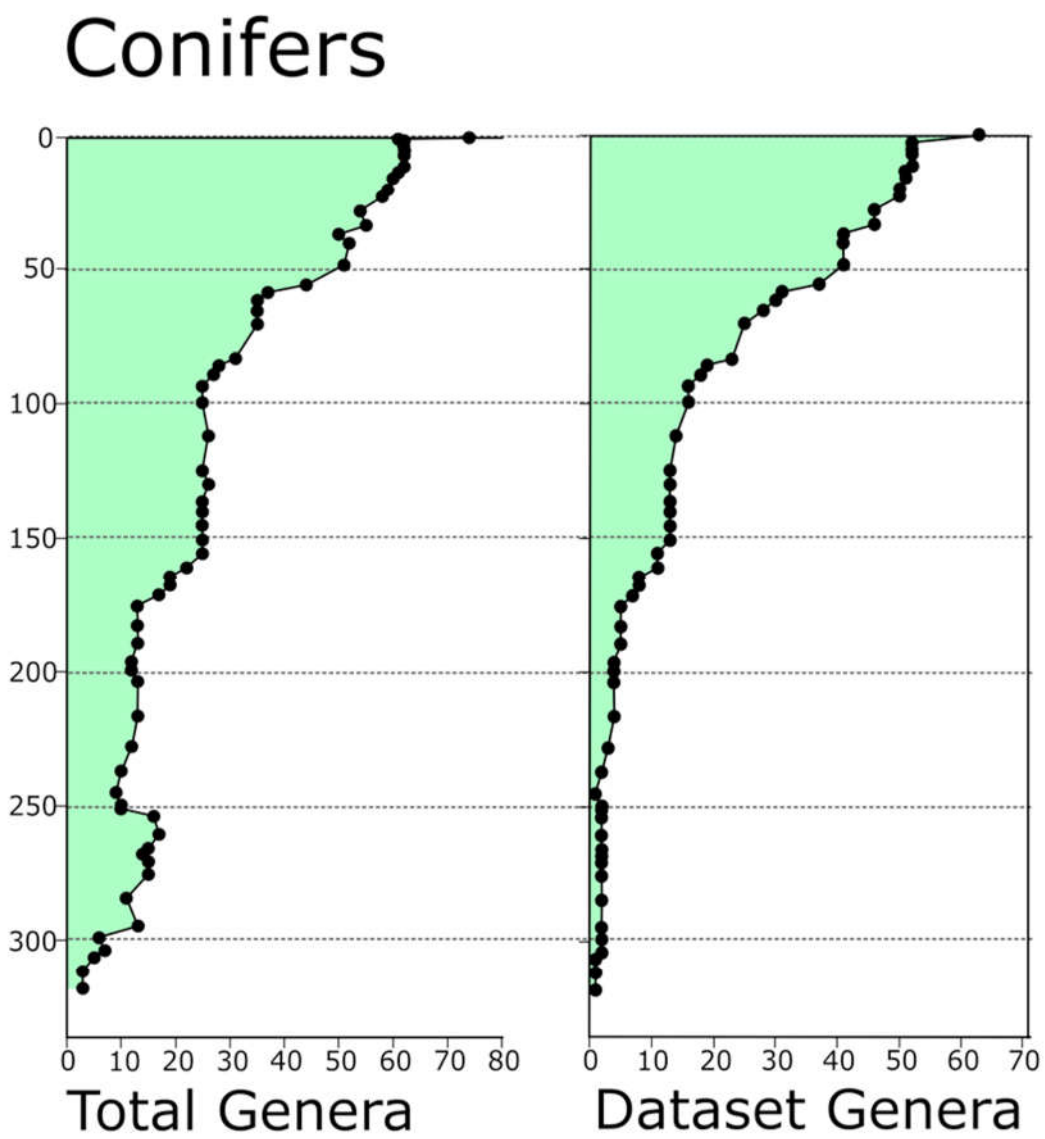
Appendix 1: Supplementary Information for 'Why should we investigate the morphological disparity of plant clades?'

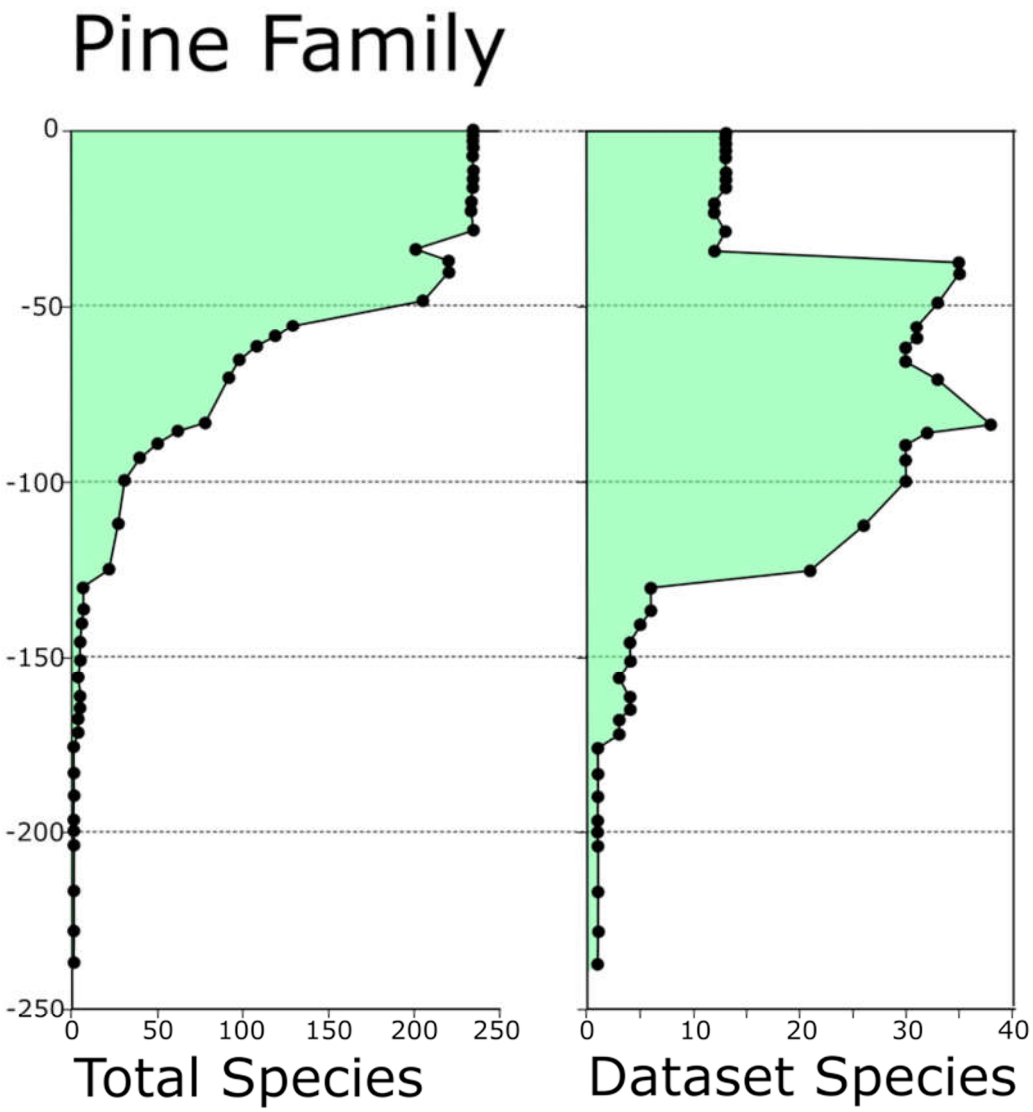
Oyston, J. W., Hughes, M., Gerber, S. & Wills, M.A. (2015). Why should we investigate the morphological disparity of plant clades? Annals of Botany, 117(5), 859-879

SUPPLEMENTARY DATA

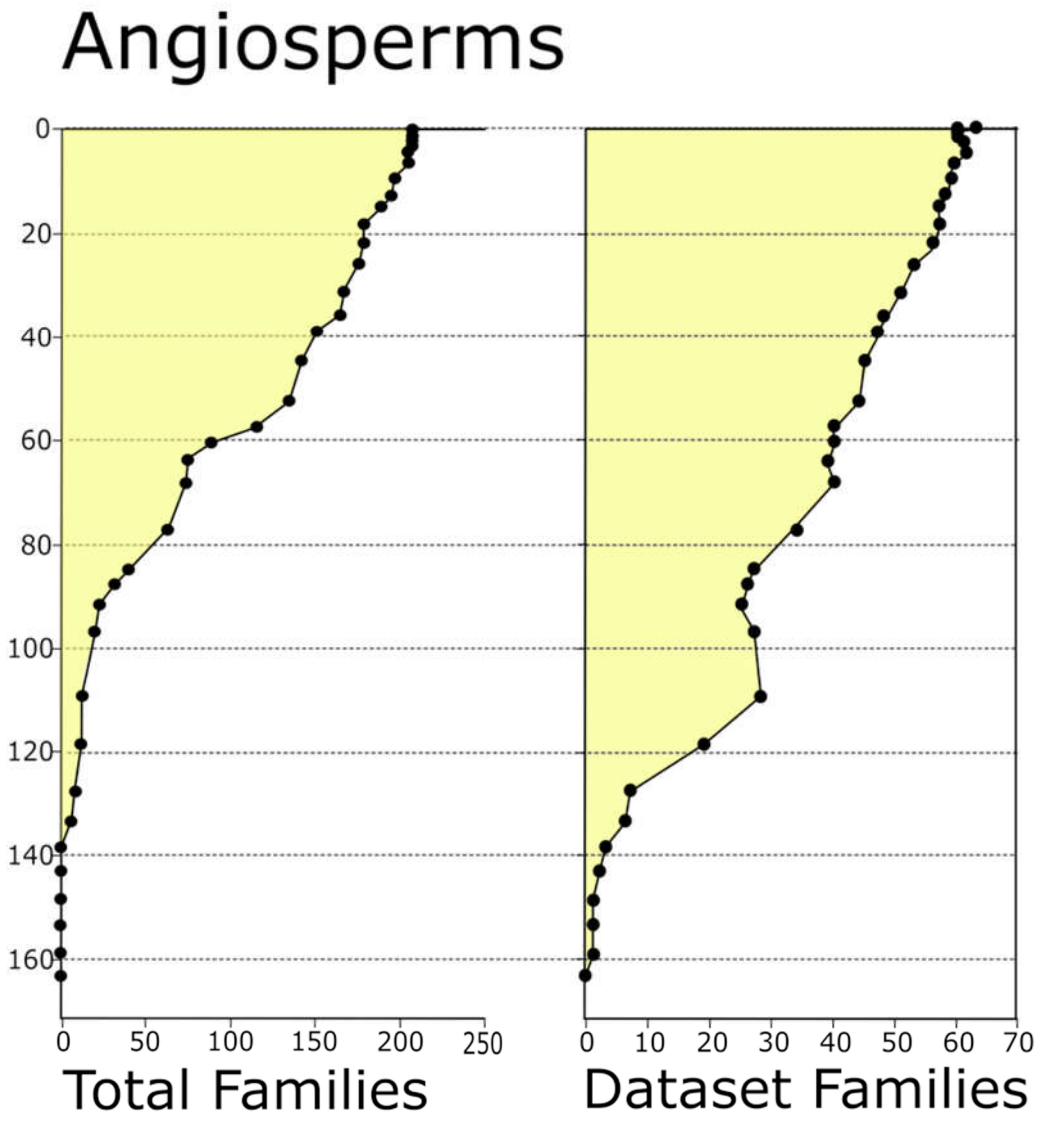
Fig. S1. Comparison between actual ('total') and sampled diversity curves



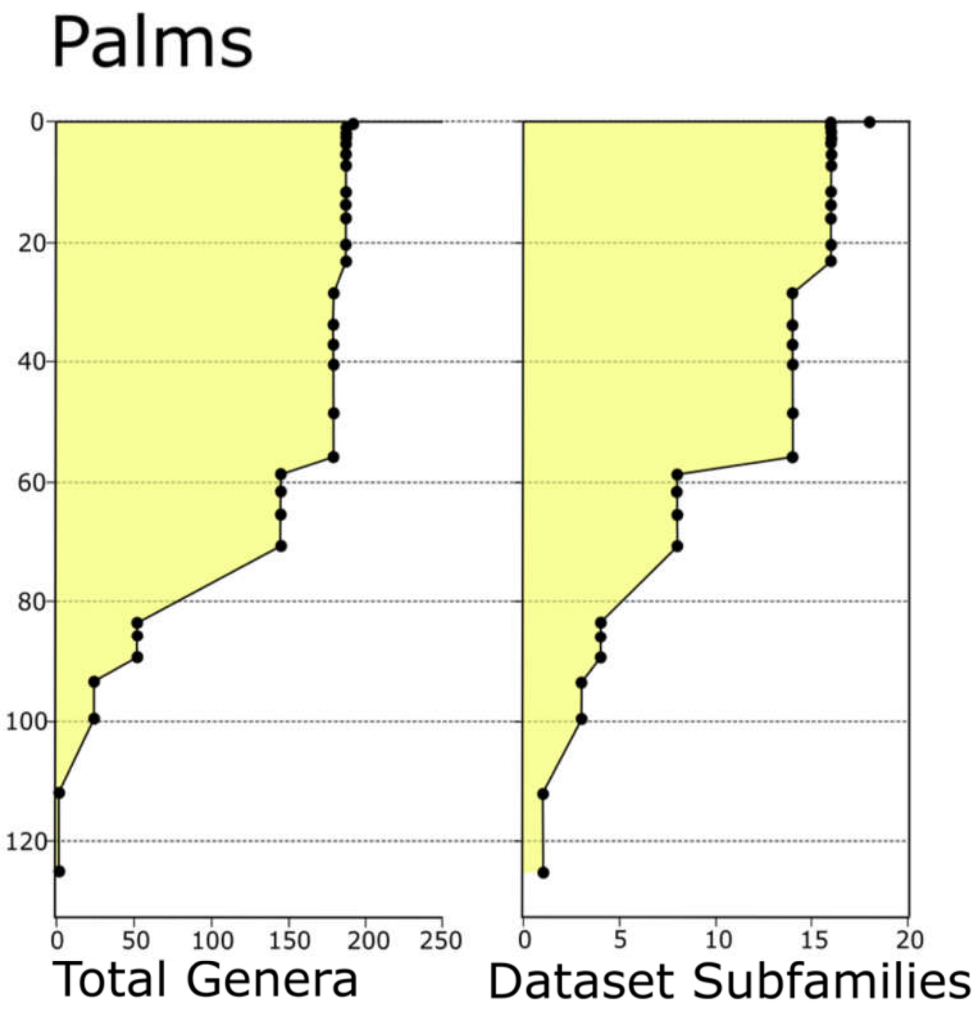
Comparison between 'total' generic diversity curves for conifers (derived from Cascales-Minana & Cleal, 2014, and the Paleobiology Database) and the genera sampled in our study (Hart, 1987).



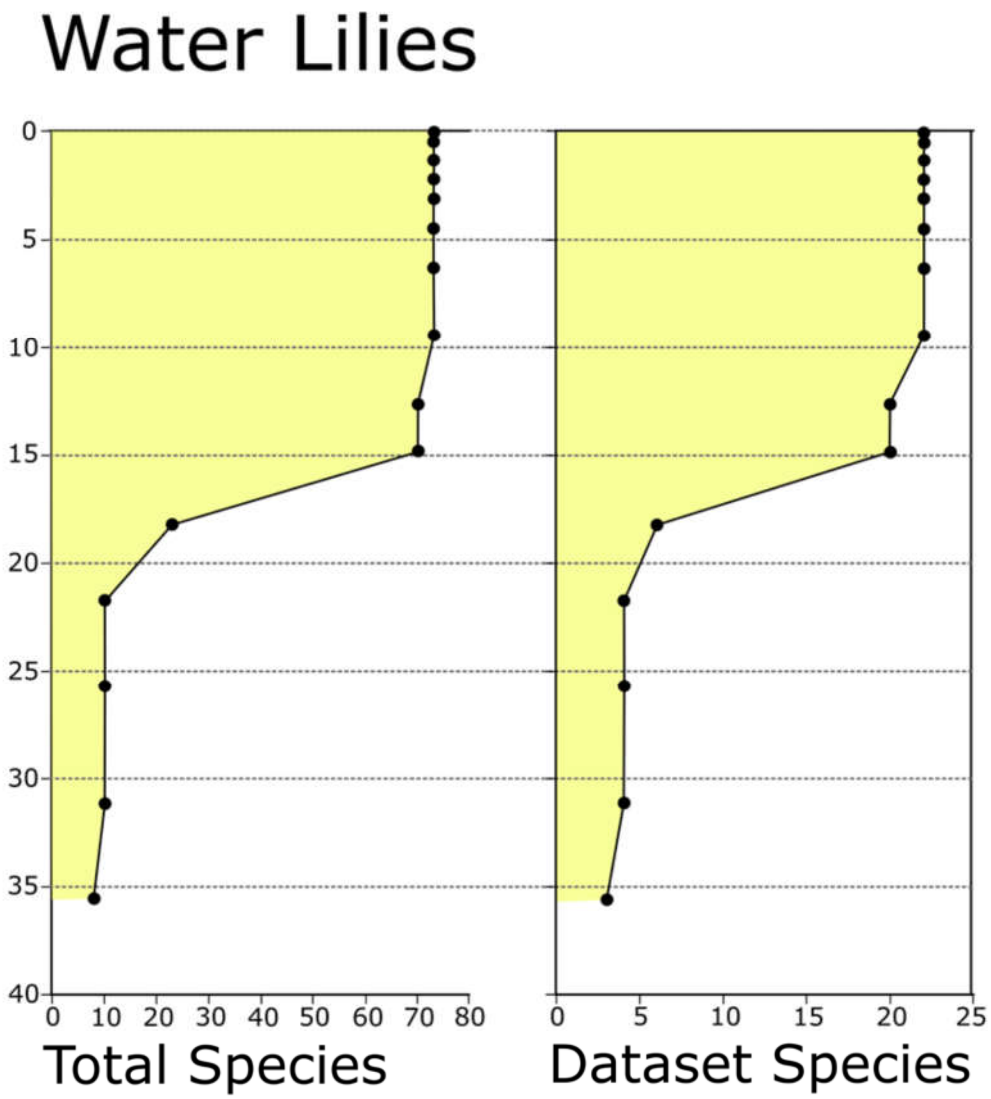
Comparison between ‘total’ species diversity curves for the pine family (derived from the Paleobiology Database) and the species sampled in our study (Klymiuk & Stockey, 2012).



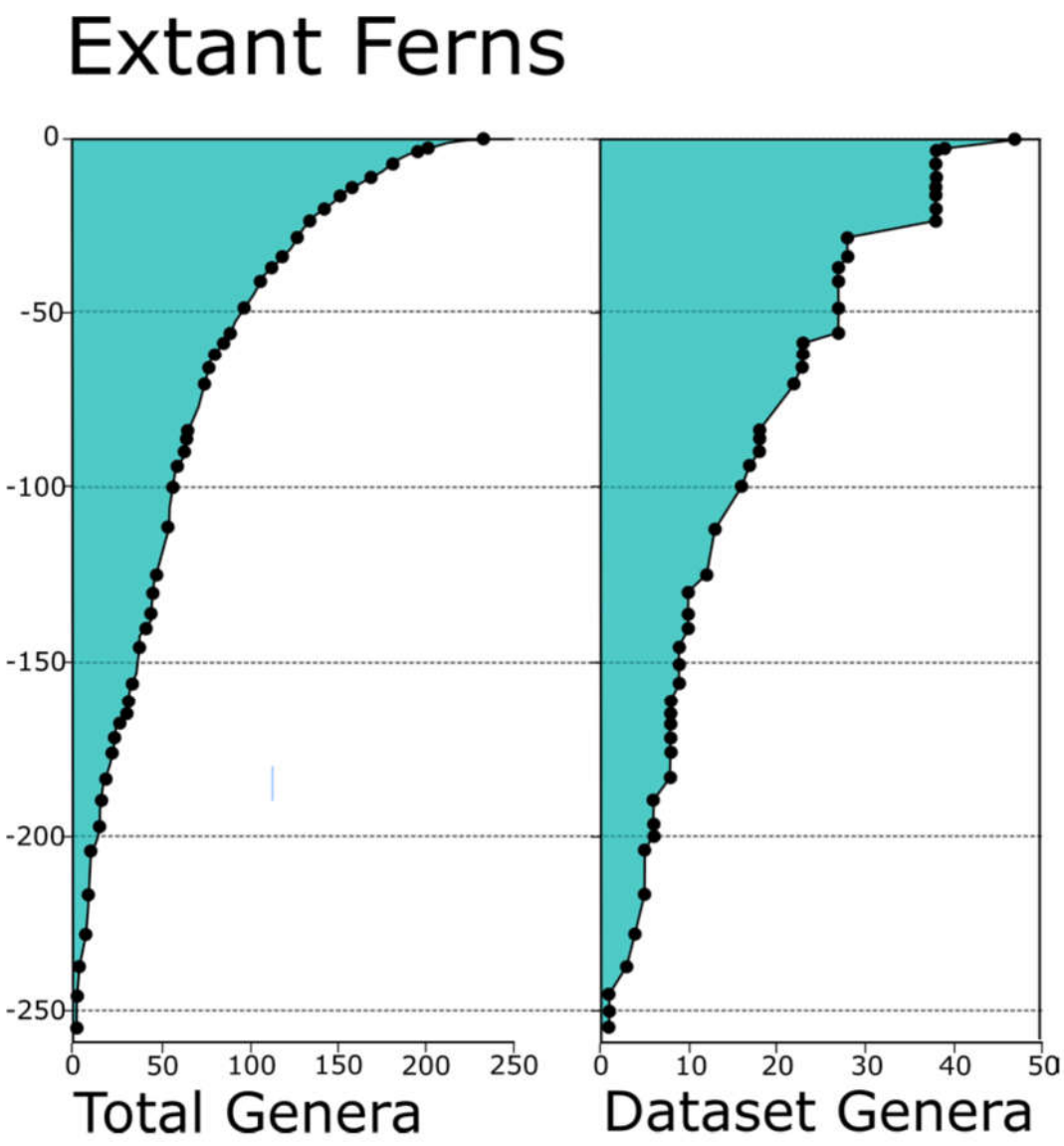
Comparison between 'total' familial diversity curves for angiosperms (derived from Cascales-Minana & Cleal, 2014) and the families sampled in our study (Doyle & Endress, 2014).



Comparison between 'total' generic diversity curves for palms (derived from Baker *et al.,* 2009, Harley, 1996 and the Paleobiology Database) and the subfamilies sampled in our study (Baker *et al.*, 2009).



Comparison between 'total' species diversity curves for water lilies (inferred from the time-calibrated molecular tree of Yoo *et al.*, 2005) and the species sampled in our study (Borsch *et al.*, 2008).



Comparison between 'total' generic diversity curves for leptosporangiate ferns (derived from the Paleobiology Database) and the genera sampled in our study (Pryer *et al.*, 1995).

Table S1. List of published disparity studies

Oyston, J. W., Hughes, M., Gerber, S. & Wills, M.A. (2015). Why should we investigate the morphological disparity of plant clades? Annals of Botany, 117(5), 859-879. https://doi.org/10.1093/aob/mcv135

Phylum	Group	Time span	Reference	Raw data
Arthropoda	Anomura	Cretaceous-Recent	Hughes et. al. (2013)	discrete characters
Arthropoda	Arachnida	U.Cambrian-Recent	Hughes et. al. (2013)	discrete characters
Arthropoda	Arthropods	Cambrian/Recent	Briggs et al. (1992)	discrete characters
Arthropoda	Arthropods	Cambrian/Carboniferous/Recent	Lofgren et. al. (2003)	discrete characters
Arthropoda	Arthropods	Cambrian/Recent	Wills et al. (1994)	discrete characters
Arthropoda	Asaphina	M.Cambrian-M.Silurian	Foote (1993a)	morphometric measurements - outlines
Arthropoda	Asaphina	M.Cambrian-M.Silurian	Foote (1993b)	morphometric measurements - outlines
Arthropoda	Asaphina	Cambrian-Ordovician	Hughes et. al. (2013)	discrete characters
Arthropoda	Asteropyginae	U.Silurian-Devonian	Hughes et. al. (2013)	discrete characters
Arthropoda	Athropoda	Cambrian/Recent	Wills (2000)	discrete characters
Arthropoda	Calymenina	Ordovician-Devonian	Foote (1993b)	morphometric measurements - outlines
Arthropoda	Cheirurina	Ordovician-Devonian	Foote (1993b)	morphometric measurements - outlines
Arthropoda	Corynexochida	Cambrian	Foote (1993b)	morphometric measurements - outlines
Arthropoda	Crustacea	Cambrian/Recent	Wills (1998a)	discrete characters
Arthropoda	Crustacea	Phanerozoic	Wills (2000)	discrete characters
Arthropoda	Crustacea	Phanerozoic	Adamowicz at al. (2008)	morphometric measurements - number and type of limb
Arthropoda	Dimeropygidae	Ordovician	Hughes et. al. (2013)	discrete characters
Arthropoda	Eodiscina	Cambrian	Hughes et. al. (2013)	discrete characters
Arthropoda	Eurypterina	U.Ordovician-L.Devonian	Hughes et. al. (2013)	discrete characters
Arthropoda	Formicidae	Cretaceous-Recent	Hughes et. al. (2013)	discrete characters
Arthropoda	Insects	Devonian-Recent	Labandeira and Eble (2007)	3 ecological descriptors
Arthropoda	Isoptera	U.Jurassic-Recent	Hughes et. al. (2013)	discrete characters
Arthropoda	Kochaspid Trilobites	Cambrian	Hughes et. al. (2013)	discrete characters
Arthropoda	Koneprusiinae	M.Ordovician-M.Devoian	Hughes et. al. (2013)	discrete characters
Arthropoda	Libristoma	Cambrian-Permian	Foote (1993a)	morphometric measurements - outlines
Arthropoda	Libristoma	Cambrian-Permian	Foote (1993b)	morphometric measurements - outlines
Arthropoda	Lichoidea	M.Cambrian-Devonian	Hughes et. al. (2013)	discrete characters
Arthropoda	Lygistorrhinidae	Cretaceous-Recent	Hughes et. al. (2013)	discrete characters
Arthropoda	Mantodea	Cretaceous-Recent	Hughes et. al. (2013)	discrete characters
Arthropoda	Mecoptera	Permian-Recent	Hughes et. al. (2013)	discrete characters
Arthropoda	Mecopteroidea	M.Permian-Recent	Hughes et. al. (2013)	discrete characters
Arthropoda	Missisquoiidae	U.Cambrian-L.Ordovician	Hughes et. al. (2013)	discrete characters
Arthropoda	Mycetophilidae	Cretaceous-Recent	Hughes et. al. (2013)	discrete characters
Arthropoda	Nematocera	M.Triassic-Recent	Hughes et. al. (2013)	discrete characters
Arthropoda	Odonata	Jurassic-Recent	Hughes et. al. (2013)	discrete characters

Arthropoda	Olenellina	L.Cambrian-M.Cambrian	Hughes et. al. (2013)	discrete characters
Arthropoda	Olenelloidea	L.Cambrian-M.Cambrian	Hughes et. al. (2013)	discrete characters
Arthropoda	Ostracod species	Eocene-recent	Hunt et al. (2010)	morphometric measurements - body size
Arthropoda	Palaeodictyoptera	E.Carboniferous-M.Permian	Hughes et. al. (2013)	discrete characters
Arthropoda	Phacopida	Ordovician-Devonian	Foote (1993a)	morphometric measurements - outlines
Arthropoda	Phacopida	Ordovician-Devonian	Foote (1993b)	morphometric measurements - outlines
Arthropoda	Phacopina	Ordovician-Devonian	Foote (1993b)	morphometric measurements - outlines
Arthropoda	Pompilidae	M.Paleogene-Recent	Hughes et. al. (2013)	discrete characters
Arthropoda	Protanisoptera	Permian	Hughes et. al. (2013)	discrete characters
Arthropoda	Proteida	Ordovician-Permian	Foote (1993a)	morphometric measurements - outlines
Arthropoda	Proteida	Ordovician-Permian	Foote (1993b)	morphometric measurements - outlines
Arthropoda	Protomyrmeleontidae	Triassic-L.Cretaceous	Hughes et. al. (2013)	discrete characters
Arthropoda	Ptychopariina	Cambrian-Ordovician	Foote (1993b)	morphometric measurements - outlines
Arthropoda	Redlichiida	Cambrian	Foote (1993b)	morphometric measurements - outlines
Arthropoda	Scutelluina	Ordovician-Devonian	Foote (1993a)	morphometric measurements - outlines
Arthropoda	Scutelluina	Ordovician-Devonian	Foote (1993b)	morphometric measurements - outlines
Arthropoda	Stylonurina	U.Ordovician-M.Permian	Hughes et. al. (2013)	discrete characters
Arthropoda	Toernquistiidae	M.Ordovician-U.Ordovician	Hughes et. al. (2013)	discrete characters
Arthropoda	Trilobita	Cambrian-Ordovician	Foote (1991b)	morphometric measurements - outlines
Arthropoda	Trilobita	Cambrian-Permian	Foote (1996b)	discrete characters
Arthropoda	Trilobite clades	Palaeozoic	Foote (1993a)	morphometric measurements - outlines
Arthropoda	Trilobite clades	Palaeozoic	Foote (1993b)	morphometric measurements - outlines
Arthropoda	Trilobites	Ordovician	Miller and Foote (1996)	morphometric measurements - outlines
Arthropoda	Trilobites	Cambrian-Permian	Webster (2007)	morphometric measurements - no. of polymorphisms
Arthropoda	Xiphosura	U.Silurian-Recent	Hughes et. al. (2013)	discrete characters
Brachiopoda	Acrotretida	Cambrian-Devonian	Smith and Bunje (1999)	morphometric measurements - ventral valve outline
Brachiopoda	Athyridida	U.Ordovician-Jurassic	Hughes et. al. (2013)	discrete characters
Brachiopoda	Billingsellidina	M.Cambrian-M.Ordovician	Hughes et. al. (2013)	discrete characters
Brachiopoda	Craniida	Phanerozoic	Smith and Bunje (1999)	morphometric measurements - ventral valve outline
Brachiopoda	Craniopsida	Ordovician-Permian	Smith and Bunje (1999)	morphometric measurements - ventral valve outline
Brachiopoda	Cryptonelloidea	Devonian-M.Permian	Hughes et. al. (2013)	discrete characters
Brachiopoda	Lingulida	Phanerozoic	Smith and Bunje (1999)	morphometric measurements - ventral valve outline
Brachiopoda	Parastrophinidae	M.Ordovician-L.Devonian	Hughes et. al. (2013)	discrete characters
Brachiopoda	Paterinida	Cambrian-Ordovician	Smith and Bunje (1999)	morphometric measurements - ventral valve outline
Brachiopoda	Rhynchonelliformea	L.Ordovician-Neogene	Ciampaglio (2004)	discrete and continuous characters
Brachiopoda	Rhynchonelliformea	L.Ordovician-Neogene	Ciampaglio (2004)	discrete and continuous characters
Brachiopoda	Siphonotretida	Cambrian-Ordovician	Smith and Bunje (1999)	morphometric measurements - ventral valve outline

Brachiopoda	Stringocephaloidea	U.Silurian-M.Permian	Hughes et. al. (2013)	discrete characters
Brachiopoda	Trimerellida	Ordovician-Devonian	Smith and Bunje (1999)	morphometric measurements - ventral valve outline
Bryozoa	Bryozoans	Ordovician	Anstey and Pachut (1995)	-
Bryozoa	Cheilostome bryozoans	Induan-Eocene	Jablonski et al. (1997)	morphometric measurements - no. of bryozoan novelties through time
Bryozoa	Cyclostome bryozoans	Induan-Maastrichtian	Jablonski et al. (1997)	morphometric measurements - no. of bryozoan novelties through time
Bryozoa	Unnamed clade	Ordovician-L.Permian	Hughes et. al. (2013)	discrete characters
Chordata	'Ecological carnivores'	Palaeocene-Recent	Wesley-Hunt (2005)	discrete characters
Chordata	Acanthodii	Devonian	Hughes et. al. (2013)	discrete characters
Chordata	Acanthomorph teleosts	E.Cretaceous-L.Miocene	Alfaro and Santini (2010)	morphometric measurements - landmarks
Chordata	Acanthomorph teleosts	E.Cretaceous-L.Miocene	Friedman (2010)	morphometric measurements - landmarks
Chordata	Agamids	Recent	Smith et. al. (2011)	morphometric measurements - body size
Chordata	Amiiformes	Jurassic-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Amphibamidae	U.Carboniferous-L.Triassic	Hughes et. al. (2013)	discrete characters
Chordata	Anatidae	M.Paleogene-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Ankylosauria	U.Jurassic-Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Anomodontia	M.Permian-M.Triassic	Hughes et. al. (2013)	discrete characters
Chordata	Anomodontia	Permian-Triassic	Ruta et. al. (2013)	discrete characters
Chordata	Aplodontoidea	M.Paleogene-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Archosauria	M.Triassic-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Archosaurs	Triassic	Brusatte et al. (2011)	discrete characters
Chordata	Arthrodira	U.Silurian-Devonian	Hughes et. al. (2013)	discrete characters
Chordata	Arthrodires	Fransian-Famennian	Anderson (2009)	morphometric measurements
Chordata	Artiodactylamorpha	U.Cretaceous-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Avemetatarsalia	Anisian-E.Jurassic	Brusatte et al. (2008a)	discrete characters
Chordata	Balistidae	L.Miocene-E.Pleistocene	Dornburg et. al. (2011)	morphometric measurements - landmarks
Chordata	Baphetoidea	Carboniferous	Hughes et. al. (2013)	discrete characters
Chordata	Borophaginae	U.Paleogene-Neogene	Hughes et. al. (2013)	discrete characters
Chordata	Bothremydidae	U.Cretaceous-M.Paleogene	Hughes et. al. (2013)	discrete characters
Chordata	Branchiosauridae	U.Carboniferous-L.Triassic	Hughes et. al. (2013)	discrete characters
Chordata	Brontotheriidae	M.Paleogene-U.Paleogene	Hughes et. al. (2013)	discrete characters
Chordata	Buchiidae	Oxfordian-Hauterivian	Grey et. Al. (2010)	morphometric measurements - measurements
Chordata	Caninae	U.Paleogene-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Carnivoramorpha	Eocene-recent	Brusatte et al. (2011)	discrete characters
Chordata	Carnivoramorpha	Eocene-recent	Brusatte et al. (2011)	discrete characters
Chordata	Carnivoramorpha	Paleogene-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Castoridae	Paleogene-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Ceratopsids	L.Campanian-Maastrichtian	Brusatte et al. (2012)	discrete characters
Chordata	Cetecea	Recent	Slater et al. (2010)	morphometric measurements - body size
Chordata	Chasmosaurinae	U.Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Cichlids	Tortonian-Recent	Coopper et al. (2010)	morphometric measurements - landmarks

Chordata	Cichlids	Chatian-Recent	Hoerner (2011)	morphometric measurements - landmarks
Chordata	Cichlids	Recent	Muschick and Indermaur (2012)	morphometric measurements - landmarks
Chordata	Coelacanths	Devonian-Carboniferous	Friedman & Coates (2006)	morphometric measurements - landmarks
Chordata	Coelurosaurs	L.Campanian-Maastrichtian	Brusatte et al. (2012)	discrete characters
Chordata	Colobinae	Recent	Tran (2014)	morphometric measurements - landmarks and measurements
Chordata	Crocodylomorpha	U.Triassic-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Crown-group Archosaurs	Anisian-Norian	Brusatte et al. (2008b)	discrete characters
Chordata	Crurotarsans	L.Triassic-L.Cretaceous	Stubbs et. al. (2013)	morphometric measurements - landmarks
Chordata	Crurotarsi	Anisian-E.Jurassic	Brusatte et al. (2008a)	discrete characters
Chordata	Crurotarsi	Anisian-Norian	Brusatte et al. (2008b)	discrete characters
Chordata	Crurotarsi	Anisian-E.Jurassic	Brusatte et al. (2010)	discrete characters
Chordata	Deinonychosauria	Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Dinosauria	Anisian-E.Jurassic	Brusatte et al. (2008a)	discrete characters
Chordata	Dinosauria	Carnian-Norian	Brusatte et al. (2008b)	discrete characters
Chordata	Dinosauria	Carnian-E.Jurassic	Brusatte et al. (2010)	discrete characters
Chordata	Dipterimorpha	Devonian-M.Permian	Hughes et. al. (2013)	discrete characters
Chordata	Eocence Euprimates	M.Eocene	Jones et al. (2013)	morphometric measurements - body size and landmarks
Chordata	Equidae	M.Paleogene-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Euarchontoglires	L.Cretaceous-Recent	Brusatte et al. (2011)	discrete characters
Chordata	Euprimateforms	Paleocene-Miocene	Hughes et. al. (2013)	discrete characters
Chordata	Eutheria	U.Cretaceous-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Galeaspida	E.Silurian-E.Devonian	Hughes et. al. (2013)	discrete characters
Chordata	Glires	Paleogene-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Gnathostomes	Ludfordian-Famenian	Anderson et al. (2011)	mixture of discrete and continuous characters
Chordata	Gorgonopsia	M.Permian-L.Permian	Hughes et. al. (2013)	discrete characters
Chordata	Hadrosauroid	L.Campanian-Maastrichtian	Brusatte et al. (2012)	discrete characters
Chordata	Hadrosauroidea	U.Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Hesperocyoninae	M.Paleogene-L.Neogene	Hughes et. al. (2013)	discrete characters
Chordata	Hyaenodontidae	E.Paleogene-M.Neogene	Hughes et. al. (2013)	discrete characters
Chordata	Ichthyopterygia	Triassic-L.Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Icthyosauria	Triassic-M.Jurassic	Thorne et. al. (2011)	discrete characters
Chordata	Iguania	Recent	Harmon et. al. (2003)	morphometric measurements - measurements
Chordata	Incisoscutoidea	M.Devonian-U.Devonian	Hughes et. al. (2013)	discrete characters
Chordata	Labyrinthodontia	U.Devonian-L.Triassic	Hughes et. al. (2013)	discrete characters
Chordata	Large carnivore guilds	Pliocene-Pleistocene	Meloro (2011)	morphometric measurements - landmarks
Chordata	Lepospondyli	Carboniferous-Permian	Hughes et. al. (2013)	discrete characters
Chordata	Limnarchia	U.Carboniferous-E.Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Mammalia	L.Triassic-L.Cretaceous	Grossnickle and Polly (2013)	morphometric measurements - landmarks
Chordata	Mammalia	Triassic-Cretaceous	Smith et. al. (2014)	discrete characters

Chordata	Marsupialia	U.Cretaceous-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Mastodonsauroidea	Triassic	Hughes et. al. (2013)	discrete characters
Chordata	Metatheria	Cretaceous-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Metriorhynchoidea	M.Jurassic-E.Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Metriorhynchoidea	Bathonian-E.Cretacaeous	Young et al. (2010)	discrete characters
Chordata	Metriorhynchoidea	Bathonian-E.Cretacaeous	Young et al. (2010)	discrete characters
Chordata	Miacoidea	Paleogene	Hughes et. al. (2013)	discrete characters
Chordata	Microsauria+Lysorophia+Nectridea+Aistopoda	E.Carboniferous-M.Permian	Hughes et. al. (2013)	discrete characters
Chordata	Mosasauridae	U.Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Multituberculata	M.Jurassic-M.Paleogene	Hughes et. al. (2013)	discrete characters
Chordata	Multituberculate	L.Jurassic-L.Cretaceous	Grossnickle and Polly (2013)	morphometric measurements - landmarks
Chordata	Mysticeti	U.Paleogene-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Non-multituberculate	M.Jurassic-L.Cretaceous	Grossnickle and Polly (2013)	morphometric measurements - landmarks
Chordata	North American Carnivores	Cenozoic	Wesley-Hunt (2005)	discrete characters
Chordata	Notosuchia	Cretaceous-M.Neogene	Hughes et. al. (2013)	discrete characters
Chordata	Omomyoidea	Paleogene	Hughes et. al. (2013)	discrete characters
Chordata	Ornithopoda	M.Jurassic-Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Osteostraci	M.Silurian-Devonian	Hughes et. al. (2013)	discrete characters
Chordata	Pachycephalosauria	U.Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Pachycephalosaurs	L.Campanian-Maastrichtian	Brusatte et al. (2012)	discrete characters
Chordata	Palmatolepis	Frasinian-Famennian	Girard and Renaud (2012)	morphometric measurements - outline
Chordata	Parasuchia	U.Triassic	Hughes et. al. (2013)	discrete characters
Chordata	Pelomedusoides	Cretaceous-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Perleidiformes	Triassic	Hughes et. al. (2013)	discrete characters
Chordata	Placodermi	Devonian	Hughes et. al. (2013)	discrete characters
Chordata	Plateosauria	Triassic-Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Plesiosauria	Jurassic-Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Plesiosaurs	L.Jurassic	Benson et al. (2012)	discrete characters
Chordata	Pliosauroidea	Jurassic-Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Procolophonidae	Triassic	Hughes et. al. (2013)	discrete characters
Chordata	Procolophonids	Triassic	Cisneros and Ruta (2010)	discrete characters
Chordata	Proviverrinae	Eocene-Miocene	Hughes et. al. (2013)	discrete characters
Chordata	Pseudopalatinae	U.Triassic	Hughes et. al. (2013)	discrete characters
Chordata	Pterasaurs	L.Triassic-L.Cretaceaous	Dyke et al. (2009)	morphometric measurements
Chordata	Pterasaurs	Traissic-Cretaceous	Prentice et al. (2011)	discrete characters
Chordata	Pteraspidiformes	U.Silurian-Devonian	Hughes et. al. (2013)	discrete characters
Chordata	Pterosauria	U.Triassic-Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Pterosauria	Triassic-Cretaceous	Smith et. al. (2014)	discrete characters
Chordata	Pterosaurs	L.Triassic-L.Cretaceaous	Butler et. al. (2011)	mixture of discrete and continuous characters

Chordata	Pterosaurs	L.Triassic-L.Cretaceaous	Foth et. al. (2012)	morphometric measurements - landmarks
Chordata	Pycnodontiformes	U.Triassic-M.Paleogene	Hughes et. al. (2013)	discrete characters
Chordata	Ratsnakes	Recent	Burbrink et. al. (2010)	morphometric measurements - body size
Chordata	Rauisuchia	M.Triassic-U.Triassic	Hughes et. al. (2013)	discrete characters
Chordata	Rhinocerotidae	M.Eocene-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Rhyncosauria	Triassic	Hughes et. al. (2013)	discrete characters
Chordata	Rodentia	M.Paleogene-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Rodentia	Recent	Vasil'ev et. al. (2010)	morphometric measurements - measurements
Chordata	Sauropoda	M.Permian-Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Selachii	Permian-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Semionotiformes	M.Triassic-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Sparoidea	M.Paleogene-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Spheniscidae	M.Paleogene-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Sphenodon	Recent	Meloro and Jones (2012)	morphometric measurements - landmarks
Chordata	Squaliformes	Cretaceous-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Squamata	M.Jurassic-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Stegosauria	M.Jurassic-L.Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Stereospondyli	M.Permian-L.Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Struthioniformes	Neogene-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Synechodontiformes	L.Devonian-L.Paleogene	Hughes et. al. (2013)	discrete characters
Chordata	Tardigrada	U.Paleogene-Recent	Hughes et. al. (2013)	discrete characters
Chordata	Teleost fish	Cretaceous-Palaeocene	Friedman (2009)	morphometric measurements
Chordata	Tetrapods	Devonian-Permian	Ruta et al. (2006)	discrete characters
Chordata	Tetrapods	Devonian-Permian	Wagner (2010)	discrete characters
Chordata	Thalattosauria	Triassic	Hughes et. al. (2013)	discrete characters
Chordata	Thelodonti	U.Ordovician-E.Devonian	Hughes et. al. (2013)	discrete characters
Chordata	Theropoda	Jurassic-Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Tyrannosauroidea	M.Jurassic-Cretaceous	Hughes et. al. (2013)	discrete characters
Chordata	Ungulates	Cenozoic	Jernvall (1996)	morphometric measurements - crown types
Chordata	Viverridae	Neogene-Recent	Hughes et. al. (2013)	discrete characters
Cnidaria	Dendrophylliidae	Cretaceous-Recent	Hughes et. al. (2013)	discrete characters
Cnidaria	Turbinoliidae	M.Cretaceous-Recent	Hughes et. al. (2013)	discrete characters
Echinodermata	Asteroidea	M.Ordovician-Recent	Hughes et. al. (2013)	discrete characters
Echinodermata	Atelostomata	Jurassic-Palaeocene	Eble (2000)	morphometric measurements - landmarks
Echinodermata	Blastoidea	M.Ordovician-Permian	Hughes et. al. (2013)	discrete characters
Echinodermata	Blastoids	Palaeozoic	Foote (1991a)	morphometric measurements - landmarks
Echinodermata	Blastoids	Palaeozoic	Foote (1993a)	morphometric measurements - landmarks
Echinodermata	Blastozoa	Cambrian-Permian	Foote (1996b)	discrete characters
Echinodermata	Blastozoans	Palaeozoic	Foote (1992)	discrete characters
Echinodermata	Blastozoans	Cambrian-Permian	Hughes et. al. (2013)	discrete characters
Echinodermata	Blastozoans	Palaeozoic	Wagner (1995a)	discrete characters

Echinodermata	Blastozons	Cambrian-Permian	Gavrilets (1999)	discrete characters
Echinodermata	Camerata	L.Ordivican-Permian	Foote (1995a)	discrete characters
Echinodermata	Camerata	L.Ordivican-Permian	Foote (1999)	discrete characters
Echinodermata	Camerata	Ordovician-Permian	Hughes et. al. (2013)	discrete characters
Echinodermata	Cinctans	M.Cambrian	Hughes et. al. (2013)	discrete characters
Echinodermata	Cladida	Ordovician-Silurian	Ausich and Deline (2012)	discrete characters
Echinodermata	Cladida	Ordovician-Silurian	Deline and Ausich (2011)	discrete characters
Echinodermata	Cladida	Ordovician-Permian	Hughes et. al. (2013)	discrete characters
Echinodermata	Cladidi & Flexibilia	L.Ordivican-Permian	Foote (1995a)	discrete characters
Echinodermata	Cladidi & Flexibilia	L.Ordivican-Permian	Foote (1999)	discrete characters
Echinodermata	Crinoidea	Ordovician-Permian	Foote (1996b)	discrete characters
Echinodermata	Crinoids	Ordovician-Silurian	Ausich and Deline (2012)	discrete characters
Echinodermata	Crinoids	Permian-L.Triassic	Ciampaglio et. al. (2001)	discrete characters
Echinodermata	Crinoids	Permian-L.Triassic	Ciampaglio et. al. (2001)	discrete characters
Echinodermata	Crinoids	Ordovician-Silurian	Deline and Ausich (2011)	discrete characters
Echinodermata	Crinoids	Ordovician-Silurian	Deline et. al. (2012)	discrete characters
Echinodermata	Crinoids	Ordovician-Devonian	Foote (1994a)	discrete characters
Echinodermata	Crinoids	Ordovician-Devonian	Foote (1994b)	discrete characters
Echinodermata	Crinoids	L.Ordivican-Permian	Foote (1995a)	discrete characters
Echinodermata	Crinoids	L.Ordivican-Permian	Foote (1995b)	discrete characters
Echinodermata	Crinoids	Palaeozoic-Post Palaeozoic	Foote (1996a)	discrete characters
Echinodermata	Crinoids	Palaeozoic-Post Palaeozoic	Foote (1999)	discrete characters
Echinodermata	Crinoids	Phanerozoic	Gerber (2013)	discrete characters
Echinodermata	Crinoids	Ordovician-Permain	Wills and Fortey (2000)	discrete characters
Echinodermata	Crown-group Echinoids	Cambrian-Recent	Hughes et. al. (2013)	discrete characters
Echinodermata	Diplobathrida	Ordovician-Silurian	Ausich and Deline (2012)	discrete characters
Echinodermata	Diplobathrida	Ordovician-Silurian	Deline and Ausich (2011)	discrete characters
Echinodermata	Disasteroida	Jurassic-M.Cretaceaous	Eble (2000)	morphometric measurements - landmarks
Echinodermata	Disparida	Ordovician-Silurian	Ausich and Deline (2012)	discrete characters
Echinodermata	Disparida	Ordovician-Silurian	Deline and Ausich (2011)	discrete characters
Echinodermata	Disparida	Ordovician-M.Permian	Hughes et. al. (2013)	discrete characters
Echinodermata	Flexibilia	M.Ordovician-Permian	Hughes et. al. (2013)	discrete characters
Echinodermata	Holasteroida	Cretaceous-Palaeocene	Eble (2000)	morphometric measurements - landmarks
Echinodermata	Holothuroidea	U.Ordovician-Recent	Hughes et. al. (2013)	discrete characters
Echinodermata	Monobathrida	Ordovician-Silurian	Ausich and Deline (2012)	discrete characters
Echinodermata	Monobathrida	Ordovician-Silurian	Deline and Ausich (2011)	discrete characters
Echinodermata	Ophiuroidea	Ordovician-Recent	Hughes et. al. (2013)	discrete characters
Echinodermata	Spatangoida	Cretaceous-Palaeocene	Eble (2000)	morphometric measurements - landmarks
Echinodermata	Spatangoida	Cretaceous	Villier and Eble (2004)	morphometric measurements - landmarks/measurements and Discrete characters
Echinodermata	Spatangoida	Cretaceous	Villier and Eble (2004)	morphometric measurements - landmarks/measurements and Discrete characters

Echinodermata	Stylophorans	M.Cambrian-M.Devonian	Lefebvre et al. (2006)	morphometric measurements - outline, measure and number of thecal plates
Hemichordata	Didymograptina	Ordovician	Hughes et. al. (2013)	discrete characters
Hemichordata	Diplograptidae	M.Ordovician-U.Ordovician	Hughes et. al. (2013)	discrete characters
Hemichordata	Eugraptoloida	L.Ordovician-M.Ordovician	Hughes et. al. (2013)	discrete characters
Hemichordata	Graptoloidea	Ordovician	Bapst et al. (2012)	mixture of discrete and continuous characters
Hemichordata	Monograptidae	M.Ordovician-Silurian	Hughes et. al. (2013)	discrete characters
Hemichordata	Orthograptidae	M.Ordovician-U.Ordovician	Hughes et. al. (2013)	discrete characters
Hemichordata	Retiolitidae	Silurian	Hughes et. al. (2013)	discrete characters
Mollusca	Ammonites	Pleisbachian-Toarcian	Dera et al. (2010)	morphometric measurements
Mollusca	Ammonites	L.Jurassic-M.Jurrassic	Gerber et al. (2008)	morphometric measurements
Mollusca	Ammonitina	Aalenian-Bathonian	Moyne and Neige (2007)	mixture of discrete and continuous characters
Mollusca	Ammonitina	Toarcian-Aalenian	Neige et al. (2001)	morphometric measurements - landmarks
Mollusca	Ammonoidea	Toarcian-Aalenian	Neige et al. (2001)	morphometric measurements - landmarks
Mollusca	Ammonoids	Permian-U.Triassic	McGowan (2004)	morphometric measurements - measurements
Mollusca	Ammonoids	Permian-U.Triassic	McGowan (2004)	morphometric measurements - measurements
Mollusca	Ammonoids	U.Carboniferous-L.Triassic	Villier and Korn (2004)	morphometric measurements - measurements
Mollusca	Anomalodesmata	Carboniferous-Recent	Hughes et. al. (2013)	discrete characters
Mollusca	Bivalvia	Cambrian-Recent	Hughes et. al. (2013)	discrete characters
Mollusca	Cardiinae	Devonian-Recent	Hughes et. al. (2013)	discrete characters
Mollusca	Conocardioids	Cambrian-Carboniferous	Wagner (1997)	discrete characters
Mollusca	Corbulidae	Palaeocene/Miocene	Anderson et al. (2010)	
Mollusca	Corbulidae	M.Palaeogene-Recent	Hughes et. al. (2013)	discrete characters
Mollusca	Euthyneura	U.Ordovician-Recent	Hughes et. al. (2013)	discrete characters
Mollusca	Gastropoda	Ordovician-Recent	Hughes et. al. (2013)	discrete characters
Mollusca	Gastropods	Palaeozoic	Wagner (1995b)	morphometric measurements - landmarks
Mollusca	Goniatitaceae	L.Devonian-M.Permian	Hughes et. al. (2013)	discrete characters
Mollusca	Goniatitids	Pennsylvanian	Saunders and Work (1996)	morphometric measurements
Mollusca	Lytoceratoidea	Jurassic-Cretaceous	Hughes et. al. (2013)	discrete characters
Mollusca	Nassariinae	Paleogene-Recent	Hughes et. al. (2013)	discrete characters
Mollusca	Pectinoidea	U.Devonian-Recent	Hughes et. al. (2013)	discrete characters
Mollusca	Pholadoidea	Jurassic-Recent	Hughes et. al. (2013)	discrete characters
Mollusca	Prolecanitids	Pennsylvanian	Saunders and Work (1996)	morphometric measurements
Mollusca	Rapaninae	M.Paleogene-Recent	Hughes et. al. (2013)	discrete characters
Mollusca	Ribeiroids	Cambrian-Silurian	Wagner (1997)	discrete characters
Mollusca	Rostrochonchs	Palaeozoic	Wagner (1997)	discrete characters
Mollusca	Scaphopoda	Devonian-Recent	Hughes et. al. (2013)	discrete characters
Mollusca	Strombid Gastropods	Mesozoic-Cenozoic	Roy (1994)	discrete characters
Mollusca	Upper Jurassic Bivalves	Oxfordian-Tithonian	Schneider et. al. (2010)	morphometric measurements - outline
Mollusca	Veneroida	Pliocene-Pleistocene	Kolbe et. al. (2011)	morphometric measurements - landmarks

Plants	Angiosperm pollen	Aptian-Palaeocene	Lupia (1999)	discrete characters
Plants	Angiosperms	Barremian-Oligocene	Crepet & Niklas (2009)	morphometric measurements - number of character states across time
Plants	Monosulcate pollen	Aptian-Maastrichtian	Lupia (1999)	discrete characters
Plants	Normapolles group pollen	Cenomanian-Maastrichtian	Lupia (1999)	discrete characters
Plants	Plants	Devonian-Permian	Boyce & Knoll (2002)	discrete characters
Plants	Triaperturate pollen	Aptian-Palaeocene	Lupia (1999)	discrete characters
Plants	Triprojectate group pollen	Campanian-Maastrichtian	Lupia (1999)	discrete characters
Priapulida	Priapulids	Cambrian/Cabinifero us/Recent	Wills (1998b)	discrete characters
Priapulida	Priapulids	Cambrian/Cabinifero us/Recent	Wills et al. (2012)	discrete characters
?	Acritarchs	Proterozoic–Cambrian	Huntley et al. (2006)	discrete characters
?	Acritarchs	Proterozoic-Cambrian	Huntley et al. (2006)	discrete characters
?	Ediacarans	Proterozoic	Shen et. Al (2008)	discrete characters

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Table S2. Distribution of characters in sampled plant data sets

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SUPPLEMENTARY DATA

Table S2. Distribution of characters in sampled plant data sets

Publication	Nandi et al. 1998	Doyle & Endress 2000	Doyle & Endress 2013	Hart 1987	Klymiuk & Stockey 2012	Pryer et al. 1995	Borsch 2008	Baker et al. 2005
Group	Extant Angiosperms	Basal Angiosperms	Angiosperms	Conifers	Pine Family	Polypod Ferns	Water Lilies	Palms
Growth & Habit	0	1	1	4	0	1	5	5
Cellular	22	0	4	2	0	2	0	6
Chemical	104	0	0	5	0	0	1	1
Stem	24	18	23	22	0	18	4	0
Leaf	17	17	13	16	0	19	7	14
Ovules/Seeds/Fruit	30	38	30	9	3	NA	6	15
Floral	37	23	54	NA	NA	0	28	52
Embryo & Development	7	0	0	27	0	1	1	3
Pollen	11	11	17	15	0	NA	10	9
Gametophyte	NA	NA	NA	NA	NA	11	NA	NA
Strobilus	NA	NA	NA	23	31	NA	NA	NA
Spores & Sporangia	NA	NA	NA	NA	NA	25	NA	NA
Total	252	108	142	123	34	52	62	105

Appendix 2: Supplementary Information for ‘What limits the morphological disparity of clades?’

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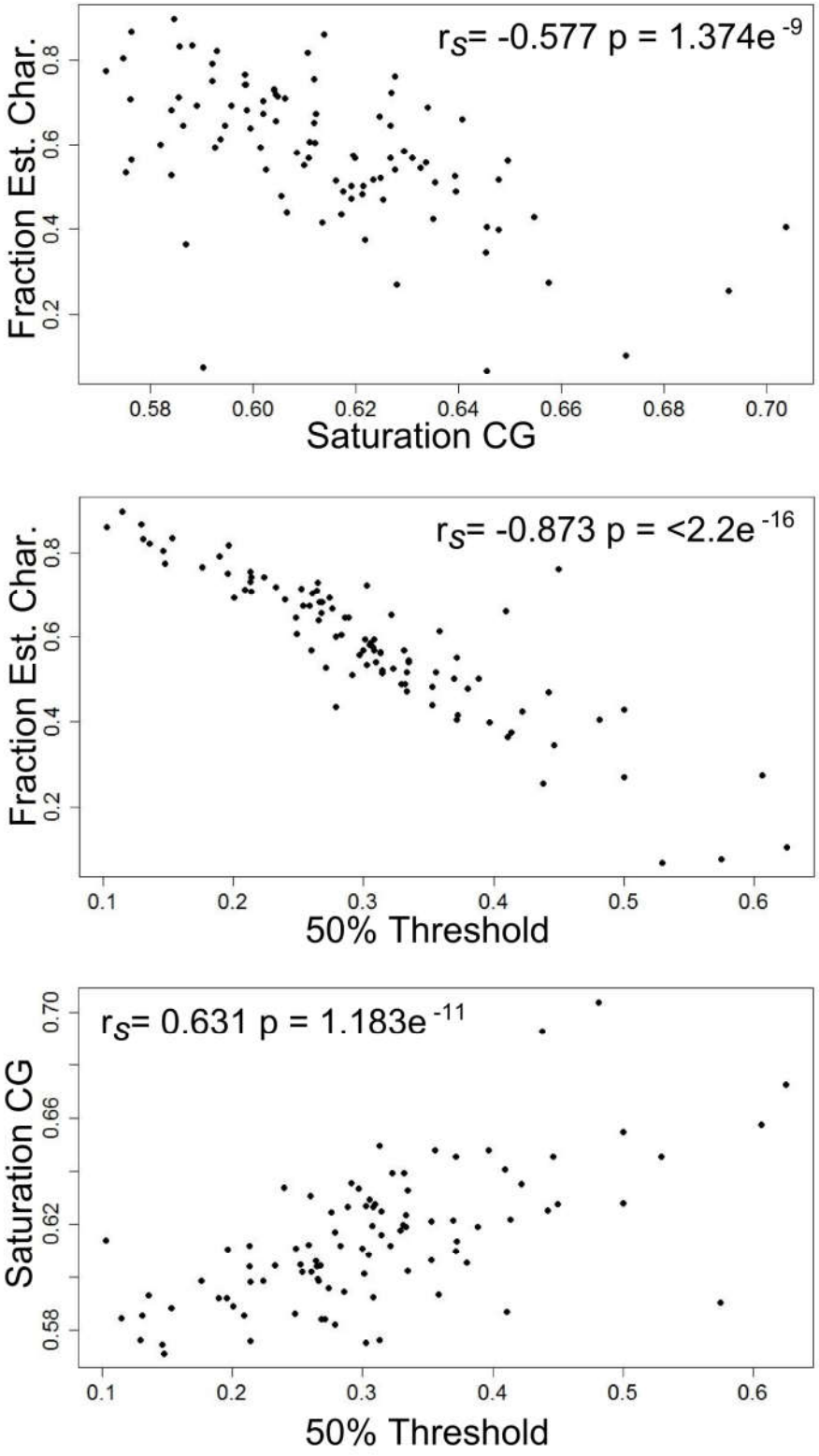
S2 Correlation between saturation indices



Appendix 3: Supplementary Information for Chapter 4

S1 List of Sources for Phylogenies

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Appendix 4: Supplementary Information for Chapter 5

S1 Table of Source Data

Clade	Subclades	Level	Taxa	Polyploid	Data
Basal Ray-fins	Lepisosteiformes	Order	33	N	Fishbase/PaleoDB
Basal Ray-fins	Acipenseriformes	Order	55	Y	Fishbase/PaleoDB
Lepidosireniformes	*Lepidosiren*	Genus	2	N	Fishbase/PaleoDB
Lepidosireniformes	*Protopterus*	Genus	8	Y	Fishbase/PaleoDB
Protacanthopterygii	Esociformes	Order	20	N	Fishbase/PaleoDB
Protacanthopterygii	Salmoniformes	Order	231	Y	Fishbase/PaleoDB
Trachichthyiformes	Trachichthyoidea	Suborder	62	N	Fishbase/PaleoDB
Trachichthyiformes	Diretmidae	Suborder	5	Y	Fishbase/PaleoDB
Cyprinodontiformes	Anablepidae	Family	18	N	Fishbase/PaleoDB
Cyprinodontiformes	Poeciliidae	Family	349	Y	Fishbase/PaleoDB
Perciformes	Anabantidae	Family	33	N	Fishbase/PaleoDB
Perciformes	Channidae	Family	39	Y	Fishbase/PaleoDB
Cyprininae 1	Cyprinion	Genus	9	N	Fishbase/PaleoDB
Cyprininae 1	Barbus sensu sricto & Aulopyge	Genus	34	Y	Fishbase/PaleoDB
Cyprininae 2	Neolissochilus	Genus	28	N	Fishbase/PaleoDB
Cyprininae 2	Labeobarbus	Genus	126	Y	Fishbase/PaleoDB
Barbinae	Enteromius	Genus	210	N	Fishbase/PaleoDB
Barbinae	Pseudobarbus	Genus	15	Y	Fishbase/PaleoDB
Cyprinidae	Spinibarbini	Tribe	7	N	Yang et al. 2015
Cyprinidae	Schizothoracini	Tribe	100	Y	Yang et al. 2015
Cyprinidae 2	Tincinae	Subfamily	10	N	Fishbase/PaleoDB
Cyprinidae 2	Leuciscinae	Subfamily	575	Y	Fishbase/PaleoDB
Cypriniformes 1	Gyrinocheilidae + Vaillantellidae	Family	6	N	Yang et al. 2015
Cypriniformes 1	Catostomidae	Family	79	Y	Yang et al. 2015
Cypriniformes 2	Nemacheilidae	Family	630	N	Yang et al. 2015
Cypriniformes 2	Cobitidae	Family	261	Y	Yang et al. 2015
Cypriniformes 3	Vaillantellidae	Family	3	N	Yang et al. 2015
Cypriniformes 3	Balitoridae + Cobitidae + Nemacheilidae	Family	990	Y	Yang et al. 2015
Characiformes	Prochilodontidae	Family	21	N	Fishbase/PaleoDB
Characiformes	Curimatidae	Family	105	Y	Fishbase/PaleoDB
Siluriformes 1	Asteroblepidae	Family	54	N	Fishbase/Kapas et al 2016/PaleoDB/Ferrais 2007
Siluriformes 1	Loricariidae	Family	719	Y	Fishbase/Kapas et al 2016/PaleoDB/Ferrais 2007
Siluriformes 2	Amblycipitidae + Sisoridae	Family	196	N	Fishbase/Kapas et al 2016/PaleoDB/Ferrais 2007
Siluriformes 2	Bagridae	Family	255	Y	Fishbase/Kapas et al 2016/PaleoDB/Ferrais 2007

Siluriformes 3	Pimelodidae	Family	97	N	Fishbase/Kapas et al 2016/PaleoDB/Ferrais 2007
Siluriformes 3	Siluridae	Family	109	Y	Fishbase/Kapas et al 2016/PaleoDB/Ferrais 2007
Siluriformes 4	Clariidae	Family	118	N	Fishbase/Kapas et al 2016/PaleoDB/Ferrais 2007
Siluriformes 4	Heteropneustidae	Family	5	Y	Fishbase/Kapas et al 2016/PaleoDB/Ferrais 2007
Siluriformes 5	Anchariidae	Family	6	N	Fishbase/Kapas et al 2016/PaleoDB/Ferrais 2007
Siluriformes 5	Ariidae	Family	166	Y	Fishbase/Kapas et al 2016/PaleoDB/Ferrais 2007
Siluriformes 6	Scoloplacidae + Asteroblepidae	Family	60	N	Fishbase/Kapas et al 2016/PaleoDB/Ferrais 2007
Siluriformes 6	Callichthyidae	Family	206	Y	Fishbase/Kapas et al 2016/PaleoDB/Ferrais 2007
Torpedinidae	Tetronarce	Genus	12	N	Fishbase/Legatt & Iwama 2003
Torpedinidae	Torpedo	Genus	11	Y	Fishbase/Legatt & Iwama 2003
Squaliformes 1	Cephaloscyllium	Genus	18	N	Fishbase/PaleoDB/Vélez-Zuazo & Agnarsson 2010
Squaliformes 1	Scyliorhinus	Genus	52	Y	Fishbase/PaleoDB/Vélez-Zuazo & Agnarsson 2010
Squaliformes 2	Scymnodon	Genus	4	N	Straube et al. 2015/Fishbase/PaleoDB
Squaliformes 2	Oxynotus	Genus	5	Y	Straube et al. 2015/Fishbase/PaleoDB
Petromyzontiformes	Geotriidae + Mordaciidae	Family	4	N	Fishbase/PaleoDB
Petromyzontiformes	Petromyzontidae	Family	42	Y	Fishbase/PaleoDB
Astylosterninae	Trichobatrachus	Genus	1	N	Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Astylosterninae	Astylosternus	Genus	12	Y	Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Bufonidae 1	Dendrophryniscus	Genus	10	N	Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Bufonidae 1	Bufo	Genus	161	Y	Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Bufonidae 2	Amietophrynus	Genus	38	N	AmphibiaWeb/Litvinchuk et al. 2016/Poynton et al. 2016/PalaeoDB
Bufonidae 2	Sclerophrys	Genus	45	Y	AmphibiaWeb/Litvinchuk et al. 2016/Poynton et al. 2016/PalaeoDB
Bombinatoridae	Barbourula	Genus	2	N	AmphibiaWeb/Litvinchuk et al. 2016/Pyron & Weins 2011/PalaeoDB
Bombinatoridae	Bombina	Genus	8	Y	AmphibiaWeb/Litvinchuk et al. 2016/Pyron & Weins 2011/PalaeoDB
Dicroglossidae	Euphlyctis	Genus	7	N	Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Dicroglossidae	Hoplobatrachus	Genus	5	Y	Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Hylidae 1	Tlalocohyla + Isthmohyla + Triprion + Anotheca + Smilisca	Genus	30	N	Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Hylidae 1	Hyla + Dryophytes	Genus	38	Y	Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Hylidae 2	Phasmahyla	Genus	7	N	Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Hylidae 2	Phyllomedusa	Genus	30	Y	Mable et al. 2011/Pyron & Weins 2011/PalaeoDB

Craugastorinae	Craugastor	Genus	110	N	Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Craugastorinae	Haddadus	Genus	3	Y	Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Holoadeninae	Bryophryne	Genus	13	N	AmphibiaWeb/Litvinchuk et al. 2016/Pyron & Weins 2011/PalaeoDB
Holoadeninae	Holoaden	Genus	4	Y	AmphibiaWeb/Litvinchuk et al. 2016/Pyron & Weins 2011/PalaeoDB
Archaeobatrachia	Ascaphus	Genus	2	N	AmphibiaWeb/Litvinchuk et al. 2016/Pyron & Weins 2011/PalaeoDB
Archaeobatrachia	Leiopelma	Genus	7	Y	AmphibiaWeb/Litvinchuk et al. 2016/Pyron & Weins 2011/PalaeoDB
Eleutherodactylinae	Diasporus	Genus	15	N	AmphibiaWeb/Otto & Whitton 2000/ Pyron & Weins 2011/PalaeoDB
Eleutherodactylinae	Eleutherodactylus	Genus	192	Y	AmphibiaWeb/Otto & Whitton 2000/ Pyron & Weins 2011/PalaeoDB
Alsodidae	Alsodes	Genus	19	N	AmphibiaWeb/Otto & Whitton 2000/ Pyron & Weins 2011/PalaeoDB
Alsodidae	Eupsophus	Genus	10	Y	AmphibiaWeb/Otto & Whitton 2000/ Pyron & Weins 2011/PalaeoDB
Pyxicephalinae	Aubria	Genus	2	N	AmphibiaWeb/Otto & Whitton 2000/ Pyron & Weins 2011/PalaeoDB
Pyxicephalinae	Pyxicephalus	Genus	4	Y	AmphibiaWeb/Otto & Whitton 2000/ Pyron & Weins 2011/PalaeoDB
Ranidae 1	Odorrana	Genus	62	N	AmphibiaWeb/Otto & Whitton 2000/ Pyron & Weins 2011/PalaeoDB
Ranidae 1	Rana	Genus	116	Y	AmphibiaWeb/Otto & Whitton 2000/ Pyron & Weins 2011/PalaeoDB
Ranidae 2	Meristogenys	Genus	13	N	AmphibiaWeb/Litvinchuk et al. 2016/Che et al. 2007/PalaeoDB
Ranidae 2	Pelophylax	Genus	26	Y	AmphibiaWeb/Litvinchuk et al. 2016/Che et al. 2007/PalaeoDB
Leiuperidae	Physalaemus + Engystomops + Edalorhina	Genus	59	N	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Leiuperidae	Pleurodema	Genus	15	Y	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Ceratophryidae	Chacophrys + Lepidobatrachus	Genus	4	N	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Ceratophryidae	Ceratophrys	Genus	8	Y	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Cycloramphibidae	Macrogenioglottus	Genus	1	N	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Cycloramphibidae	Odontophrynus	Genus	11	Y	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Microhylidae 1	Elachistocleis + Hamptophryne + Gastrophryne	Genus	23	N	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Microhylidae 1	Chiasmocleis	Genus	20	Y	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Microhylidae 2	Barygenys	Genus	9	N	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB

Microhylidae 2	Cophixalus	Genus	61	Y	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Microhylidae 3	Paradoxophyla	Genus	2	N	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Microhylidae 3	Scaphiophryne	Genus	9	Y	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Pipidae 1	Silurana	Genus	2	N	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Pipidae 1	Xenopus	Genus	22	Y	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Pipidae 2	Hymenochirus	Genus	4	N	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Pipidae 2	Silurana + Xenopus	Genus	24	Y	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Lymnodynastidae	Notaden	Genus	4	N	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Lymnodynastidae	Neobatrachus	Genus	10	Y	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Pyxicephalidae 1	Strongylopus + Poyntonia + Microbatrachella + Cacosternum	Genus	29	N	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Pyxicephalidae 1	Tomopterna	Genus	15	Y	AmphibiaWeb/Mable et al. 2011/Pyron & Weins 2011/PalaeoDB
Salamandroidea	Dicamptodon	Genus	6	N	AmphibiaWeb/Otto & Whitton 2000/ Pyron & Weins 2011/PalaeoDB
Salamandroidea	Ambystoma	Genus	33	Y	AmphibiaWeb/Otto & Whitton 2000/ Pyron & Weins 2011/PalaeoDB
Pleurodelinae 1	Calotriton	Genus	2	N	AmphibiaWeb/Zhang et al. 2008/ Pyron & Weins 2011/PalaeoDB
Pleurodelinae 1	Triturus	Genus	11	Y	AmphibiaWeb/Zhang et al. 2008/ Pyron & Weins 2011/PalaeoDB
Pleurodelinae 2	Mesotriton	Genus	10	N	AmphibiaWeb/Zhang et al. 2008/ Pyron & Weins 2011/PalaeoDB
Pleurodelinae 2	Lissotriton	Genus	10	Y	AmphibiaWeb/Zhang et al. 2008/ Pyron & Weins 2011/PalaeoDB
Urodela	Salamandroidea + Cryptobranchoidea	Family	520	N	AmphibiaWeb/Otto & Whitton 2000/ Pyron & Weins 2011/PalaeoDB
Urodela	Sirenidae	Family	16	Y	AmphibiaWeb/Otto & Whitton 2000/ Pyron & Weins 2011/PalaeoDB
Amphibolurinae	Lophognathus	Genus	5	N	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Amphibolurinae	Amphibolurus	Genus	7	Y	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Agamidae	Hydrosaurus +Amphibolurinae	Genus	121	N	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Agamidae	Leiolepis	Genus	9	Y	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB

Gekkonidae 1	Hemiphyllodactylus	Genus	19	N	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Gekkonidae 1	Gehyra	Genus	48	Y	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Gekkonidae 2	Cyrtodactylus	Genus	232	N	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Gekkonidae 2	Hemidactylus	Genus	144	Y	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Gekkonidae 3	Dixonius	Genus	8	N	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Gekkonidae 3	Heteronotia	Genus	5	Y	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Gekkonidae 4	Luperosaurus	Genus	13	N	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Gekkonidae 4	Lepidodactylus	Genus	33	Y	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Iguanidae	Urosaurus	Genus	26	N	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Iguanidae	Sceloporus	Genus	101	Y	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Lacertinae	Timon	Genus	6	N	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Lacertinae	Lacerta	Genus	45	Y	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Teiidae 1	Ameiva	Genus	36	N	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Teiidae 1	Cnemidophorus	Genus	59	Y	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Typhlopidae	Anilios	Genus	46	N	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Typhlopidae	Indotyphlops	Genus	24	Y	Otto & Whitton 2000/Pyron et al. 2013/The Reptile Database/PalaeoDB
Chelidae	Acanthochelys	Genus	4	N	Otto & Whitton 2000/Seddon et al. 1997/The Reptile Database/PalaeoDB
Chelidae	Platemys	Genus	1	Y	Otto & Whitton 2000/Seddon et al. 1997/The Reptile Database/PalaeoDB

Viperidae	Crotalus + Sistrurus	Genus	47	N	Tiersch et al. 1991/Wuster et al. 2008/The Reptile Database/PalaeoDB
Viperidae	Agkistrodon	Genus	6	Y	Tiersch et al. 1991/Wuster et al. 2008/The Reptile Database/PalaeoDB
Typhlopidae	Acutotyphlops	Genus	4	N	Tiersch et al. 1991/Pyron & Wiens 2013/The Reptile Database/PalaeoDB
Typhlopidae	Ramphotyphlops	Genus	49	Y	Tiersch et al. 1991/Pyron & Wiens 2013/The Reptile Database/PalaeoDB
Teiidae 2	Ameiva	Genus	7	N	Schon et al. 2009/Pyron & Wiens 2013/The Reptile Database/PalaeoDB
Teiidae 2	Aspidoscelis	Genus	11	Y	Schon et al. 2009/Pyron & Wiens 2013/The Reptile Database/PalaeoDB
Gymnophthalmidae	Arthrosaura	Genus	2	N	Schon et al. 2009/Pyron & Wiens 2013/The Reptile Database/PalaeoDB
Gymnophthalmidae	Leposoma	Genus	6	Y	Schon et al. 2009/Pyron & Wiens 2013/The Reptile Database/PalaeoDB
Scincidae	Emoia	Genus	15	N	Schon et al. 2009/Pyron & Wiens 2013/The Reptile Database/PalaeoDB
Scincidae	Menetia	Genus	6	Y	Schon et al. 2009/Pyron & Wiens 2013/The Reptile Database/PalaeoDB
Tropiduridae	Phymaturus	Genus	47	N	Lamborot et al. 2006/Pyron & Wiens 2013/The Reptile Database/PalaeoDB
Tropiduridae	Liolaemus	Genus	256	Y	Lamborot et al. 2006/Pyron & Wiens 2013/The Reptile Database/PalaeoDB
Phasianinae	Bambosicola	Genus	3	N	Otto & Whitton 2000/Eo et al. 2009/Avibase/PalaeoDB
Phasianinae	Gallus	Genus	14	Y	Otto & Whitton 2000/Eo et al. 2009/Avibase/PalaeoDB
Arini	Primolius	Genus	3	N	Otto & Whitton 2000/Tavares et al. 2006/Avibase/PalaeoDB
Arini	Ara	Genus	10	Y	Otto & Whitton 2000/Tavares et al. 2006/Avibase/PalaeoDB
Octodontidae	Otomys	Genus	28	N	Otto & Whitton 2000/Honeycutt et al. 2003/Mammal Species of the World/PalaeoDB
Octodontidae	Tympanoctomys	Genus	4	Y	Otto & Whitton 2000/Honeycutt et al. 2003/Mammal Species of the World/PalaeoDB
Ptininae	Sphaericus	Genus	1	N	Otto & Whitton 2000/Phillips 2000/Catalogue of Life/PalaeoDB
Ptininae	Ptinus	Genus	42	Y	Otto & Whitton 2000/Phillips 2000/Catalogue of Life/PalaeoDB
Eumolpinae	Colasposoma	Genus	5	N	Otto & Whitton 2000/Gomez-Zurita 2007/BioLib/PalaeoDB
Eumolpinae	Bromius	Genus	2	Y	Otto & Whitton 2000/Gomez-Zurita 2007/Catalogue of Life/PalaeoDB

Alticini	Aphthona	Genus	7	N	Otto & Whitton 2000/Gillespie et al. 2008/Catalogue of Life/PalaeoDB
Alticini	Altica	Genus	74	Y	Otto & Whitton 2000/Gillespie et al. 2008/Catalogue of Life/PalaeoDB
Doryphorina	Zygogramma	Genus	13	N	Otto & Whitton 2000/Gomez Zurita 2007/BugGuide/PalaeoDB
Doryphorina	Calligrapha	Genus	38	Y	Otto & Whitton 2000/Gomez Zurita 2007/BugGuide/PalaeoDB
Curculionoidea	Brentidae	Family	1758	N	Otto & Whitton 2000/Haran 2013/Catalogue of Life/PalaeoDB
Curculionoidea	Curculionidae	Family	82320	Y	Otto & Whitton 2000/Haran 2013/Catalogue of Life/PalaeoDB
Xyleborini	Theoborus + Coptoborus + Sampsonius + Dryocoetoides	Genus	100	N	Smith 1971/Jordal 2002/Catalogue of Life/PalaeoDB
Xyleborini	Xyleborus	Genus	1524	Y	Smith 1971/Jordal 2002/Catalogue of Life/PalaeoDB
Ipini	Pityogenes	Genus	40	N	Smith 1971/Cognato 2000/Catalogue of Life/PalaeoDB
Ipini	Orthotomicus + Ips	Genus	235	Y	Smith 1971/Cognato 2000/Catalogue of Life/PalaeoDB
Pityophthorina	Conophthorus	Genus	25	N	Smith 1971/Cognato et al. 2005/Catalogue of Life/PalaeoDB
Pityophthorina	Pityophthorus	Genus	548	Y	Smith 1971/Cognato et al. 2005/Catalogue of Life/PalaeoDB
Scolytinae	Hylesinopsis + Haplogenius + Strombophorus + Ctonoxylon + Hypothenemus + Hylesinus	Genus	650	N	Smith 1971/Jordal et al. 2007/Catalogue of Life/PalaeoDB
Scolytinae	Dendroctonus	Genus	47	Y	Smith 1971/Jordal et al. 2007/Catalogue of Life/PalaeoDB
Chrysomelinae	Zygogramma	Genus	13	N	Smith 1971/Gomez-Zurita et al. 2008/Catalogue of Life/PalaeoDB
Chrysomelinae	Calligrapha	Genus	37	Y	Smith 1971/Gomez-Zurita et al. 2008/Catalogue of Life/PalaeoDB
Archostemata	Crowsoniella	Genus	1	N	Smith 1971/Beutel et al. 2008/Catalogue of Life/PalaeoDB
Archostemata	Micromalthus	Genus	4	Y	Smith 1971/Beutel et al. 2008/Catalogue of Life/PalaeoDB
Blosyrini	Blosyrodes + Blosyrosoma + Bradybamon + Dactylotus + Holonychus + Proscephaladeres	Genus	73	N	Smith 1971/Mavladi 1998/Catalogue of Life/PalaeoDB
Blosyrini	Blosyrus	Genus	85	Y	Smith 1971/Mavaldi 1998/Catalogue of Life/PalaeoDB
Listroderini	Methypora + Rupanius + Acrorius + Trachoderma + Lamiarhinus + Philippius + Germainiellus	Genus	32	N	Smith 1971/Morrone 2013/Catalogue of Life/PalaeoDB
Listroderini	Listroderes	Genus	183	Y	Smith 1971/Morrone 2013/Catalogue of Life/PalaeoDB
Entiminae	Naupactus + Barynotus + Strophosoma + Liophloeus + Polydrusus	Genus	538	N	Otto & Whitton 2000/Haran

					2013/Catalogue of Life/PalaeoDB
Entiminae	Otiorhynchus	Genus	1288	Y	Otto & Whitton 2000/Haran 2013/Catalogue of Life/PalaeoDB
Naupactini	Pantomorus	Genus	36	N	Otto & Whitton 2000/Normark & Lanteri 1998/Catalogue of Life/PalaeoDB
Naupactini	Arimigus	Genus	8	Y	Otto & Whitton 2000/Normark & Lanteri 1998/Catalogue of Life/PalaeoDB
Chamaemyiidae	Leucopinae	Subfamily	183	N	Otto & Whitton 2000/Tree of Life/Catalogue of Life/PalaeoDB
Chamaemyiidae	Chamaemyiinae	Subfamily	165	Y	Otto & Whitton 2000/Tree of Life/Catalogue of Life/PalaeoDB
Orthocladinae 1	Mesosmittia	Genus	16	N	Otto & Whitton 2000/Cranston et al. 2011/Systema Dipterorum/PalaeoDB
Orthocladinae 1	Limnophyes	Genus	141	Y	Otto & Whitton 2000/Cranston et al. 2011/Systema Dipterorum/PalaeoDB
Tanytarsini	Tanytarsus	Genus	470	N	Otto & Whitton 2000/Ekrem et al. 2010/Systema Dipterorum/PalaeoDB
Tanytarsini	Paratanytarsus	Genus	69	Y	Otto & Whitton 2000/Ekrem et al. 2010/Systema Dipterorum/PalaeoDB
Orthocladiinae 2	Ferringtonia	Genus	1	N	Otto & Whitton 2000/Cranston et al. 2011/Systema Dipterorum/PalaeoDB
Orthocladiinae 2	Pseudosmittia	Genus	93	Y	Otto & Whitton 2000/Cranston et al. 2011/Systema Dipterorum/PalaeoDB
Agromyzidae	Napomyza	Genus	79	N	Otto & Whitton 2000/Scheffer et al. 2007/Systema Dipterorum/PalaeoDB
Agromyzidae	Phytomyza + Chromatomyia	Genus	703	Y	Otto & Whitton 2000/Scheffer et al. 2007/Systema Dipterorum/PalaeoDB
Psychodini	Psychomora	Genus	1	N	Otto & Whitton 2000/Espindola et al. 2012/Systema Dipterorum/PalaeoDB
Psychodini	Psychoda	Genus	365	Y	Otto & Whitton 2000/Espindola et al. 2012/Systema Dipterorum/PalaeoDB
Simuliini	Stegopterna	Genus	15	N	Otto & Whitton 2000/Espindola et al. 2012/Systema Dipterorum/PalaeoDB
Simuliini	Cnephia	Genus	12	Y	Otto & Whitton 2000/Espindola et al. 2012/Systema Dipterorum/PalaeoDB
Prosimuliini 2	Pedrowygomyia	Genus	4	N	Otto & Whitton 2000/Coscaron et al. 1998/Encyclopedia of Life/PalaeoDB

Prosimuliini 2	Prosimulium	Genus	160	Y	Otto & Whitton 2000/Coscaron et al. 1998/Encyclopedia of Life/PalaeoDB
Oligotomidae	Oligotoma	Genus	25	N	Otto & Whitton 2000/Miller et al. 2012/Catalogue of Life/PalaeoDB
Oligotomidae	Haploembia	Genus	10	Y	Otto & Whitton 2000/Miller et al. 2012/Verhoeff 1904/PalaeoDB
Coccidae	Eulecanium	Genus	50	N	Otto & Whitton 2000/Choi 2016/Catalogue of Life/PalaeoDB
Coccidae	Physokermes	Genus	11	Y	Otto & Whitton 2000/Choi 2016/Catalogue of Life/PalaeoDB
Delphacidae	Nilaparvata	Genus	17	N	Otto & Whitton 2000/Urban et al. 2010/Catalogue of Life/PalaeoDB
Delphacidae	Muellerianella	Genus	7	Y	Otto & Whitton 2000/Urban et al. 2010/Catalogue of Life/PalaeoDB
Diprionidae	Neoprion	Genus	14	N	Otto & Whitton 2000/Malm & Nyman 2015/Catalogue of Life/PalaeoDB
Diprionidae	Diprion	Genus	3	Y	Otto & Whitton 2000/Malm & Nyman 2015/Catalogue of Life/PalaeoDB
Apidae	Scaura	Genus	5	N	Otto & Whitton 2000/Costa et al. 2003/Catalogue of Life/PalaeoDB
Apidae	Melipona	Genus	63	Y	Otto & Whitton 2000/Costa et al. 2003/Catalogue of Life/PalaeoDB
Psychidae	Siederia	Genus	8	N	Otto & Whitton 2000/Chevasco et al. 2014/Sobczyk 2011/PalaeoDB
Psychidae	Dahlica	Genus	45	Y	Otto & Whitton 2000/Chevasco et al. 2014/Weidlich 2016/PalaeoDB
Blaberidae 1	Epilampra	Genus	70	N	Otto & Whitton 2000/Kambhampati 1995/Catalogue of Life/PalaeoDB
Blaberidae 1	Pycnoscelus	Genus	15	Y	Otto & Whitton 2000/Kambhampati 1995/Catalogue of Life/PalaeoDB
Blaberidae 2	Blaberus	Genus	6	N	Otto & Whitton 2000/Kambhampati 1995/Catalogue of Life/PalaeoDB
Blaberidae 2	Eublaberus	Genus	9	Y	Otto & Whitton 2000/Kambhampati 1995/Catalogue of Life/PalaeoDB
Tettigoniidae	Clonia + Cloniella + Peringueyella	Genus	27	N	Otto & Whitton 2000/Giannoulis et al. 2011/Catalogue of Life/PalaeoDB
Tettigoniidae	Saga	Genus	15	Y	Otto & Whitton 2000/Giannoulis et al.

					2011/Catalogue of Life/PalaeoDB
Crassiclitellata 1	Hormogastridae	Family	31	N	Viktorov 1997/James & Davidson 2012/Encyclopedia of Life/PalaeoDB
Crassiclitellata 1	Lumbricidae	Family	251	Y	Viktorov 1997/James & Davidson 2012/Encyclopedia of Life/PalaeoDB
Crassiclitellata 2	Acanthodrilidae	Family	193	N	Shen et al. 2011, Murchie 1967/James & Davidson 2012/Encyclopedia of Life/PalaeoDB
Crassiclitellata 2	Megascolecidae	Family	467	Y	Shen et al. 2011, Murchie 1967/James & Davidson 2012/Encyclopedia of Life/PalaeoDB
Naididae	Phallodrilinae + Rhyacodrilinae	Subfamily	750	N	Christensen 1980a/Erseus et al. 2002/WoRMS/PalaeoDB
Naididae	Tubificinae	Subfamily	723	Y	Christensen 1980a/Erseus et al. 2002/WoRMS/PalaeoDB
Tubificinae	Limnodrilus	Genus	70	N	Marotta et al. 2014/Beauchamp et al. 2001/WoRMS/PalaeoDB
Tubificinae	Tubifex	Genus	91	Y	Marotta et al. 2014/Beauchamp et al. 2001/WoRMS/PalaeoDB
Lumbricidae 1	Allolobophora	Genus	12	N	Gregory & Hebert /Perez-Losada et al. 2011/WoRMS/PalaeoDB
Lumbricidae 1	Dendrobaena	Genus	16	Y	Gregory & Hebert /Perez-Losada et al. 2011/WoRMS/PalaeoDB
Megascolecidae 1	Begemius	Genus	6	N	Shen et al. 2011/Buckley et al. 2011/ITIS/PalaeoDB
Megascolecidae 1	Amynthas	Genus	488	Y	Shen et al. 2011/Buckley et al. 2011/ITIS/PalaeoDB
Lumbricidae 2	Postandrilus	Genus	6	N	Shen et al. 2011/Csuzdi et al. 2017/Encyclopedia of Life/PalaeoDB
Lumbricidae 2	Aporrectodea	Genus	46	Y	Shen et al. 2011/Csuzdi et al. 2017/Encyclopedia of Life/PalaeoDB
Lumbricidae 3	Eiseniona	Genus	3	N	Shen et al. 2011/Csuzdi et al. 2017/Encyclopedia of Life/PalaeoDB
Lumbricidae 3	Eiseniella	Genus	6	Y	Shen et al. 2011/Csuzdi et al. 2017/Diaz Cosin et al. 2014/PalaeoDB
Lumbricidae 4	Octodrilus	Genus	40	N	Shen et al. 2011/Csuzdi et al. 2017/Encyclopedia of Life/PalaeoDB
Lumbricidae 4	Octolasion	Genus	5	Y	Shen et al. 2011/Csuzdi et al. 2017/Encyclopedia of Life/PalaeoDB
Megascolecidae 2	Trigaster + Neotrigaster	Genus	33	N	Shen et al. 2011/Buckley et al. 2011/Encyclopedia of Life/PalaeoDB
Megascolecidae 2	Diplocardia	Genus	48	Y	Shen et al. 2011/Buckley et al. 2011/Encyclopedia of Life/PalaeoDB
Enchytraeidae	Grania	Genus	87	N	Christensen 1980b/Erseus et al. 2010/WoRMS/PalaeoDB
Enchytraeidae	Lumbricillus	Genus	113	Y	Christensen 1980b/Erseus et al. 2010/WoRMS/PalaeoDB
Pontoporeiidae	Monoporeia + Diporeia	Genus	3	N	Song et al. 2012/WoRMS/PalaeoDB

Pontoporeiidae	Pontoporeia	Genus	13	Y	Song et al. 2012/WoRMS/PalaeoDB
Anostraca	Parartemia	Genus	2	N	Song et al. 2012/Weekers et al. 2002/Encyclopedia of Life/PalaeoDB
Anostraca	Artemia	Genus	10	Y	Song et al. 2012/Weekers et al. 2002/Encyclopedia of Life/PalaeoDB
Cambaridae	Troglocambarus	Genus	1	N	Martin et al. 2016/Crandall & De Grave et al. 2017/ITIS/PalaeoDB
Cambaridae	Procambarus	Genus	160	Y	Martin et al. 2016/Crandall & De Grave et al. 2017/ITIS/PalaeoDB
Daphniidae	Simocephalus	Genus	30	N	Beaton et al. 1988/Stenderup et al. 2006/Encyclopedia of Life/PalaeoDB
Daphniidae	Daphnia	Genus	38	Y	Beaton et al. 1988/Stenderup et al. 2006/ITIS/PalaeoDB
Phronimidae	Phronimella	Genus	1	N	Larval et al. 1975/ITIS/PalaeoDB
Phronimidae	Phronima	Genus	10	Y	Larval et al. 1975/ITIS/PalaeoDB
Trichoniscidae	Haplophthalmus + Oritoniscus	Genus	76	N	Song et al. 2012/Michel-Salzat 2000/ITIS/PalaeoDB
Trichoniscidae	Trichoniscus	Genus	125	Y	Song et al. 2012/Michel-Salzat 2000/ITIS/PalaeoDB
Ascarididae	Ascaris	Genus	2	N	Song et al. 2012/Nadler 1992/ITIS/PalaeoDB
Ascarididae	Parascaris	Genus	1	Y	Song et al. 2012/Nadler 1992/ITIS/PalaeoDB
Cerithioidea	Paludomidae	Family	104	N	Song et al. 2012/Strong et al. 2011/WMSDB/PalaeoDB
Cerithioidea	Thiaridae	Family	289	Y	Song et al. 2012/Strong et al. 2011/WMSDB/PalaeoDB
Ancylini	Ferrissia	Genus	60	N	Song et al. 2012/Albrecht et al. 2007/WMSDB/PalaeoDB
Ancylini	Ancylus	Genus	31	Y	Song et al. 2012/Albrecht et al. 2007/WMSDB/PalaeoDB
Mytilidae	Perna + Perumytilus + Rhomboidella + Semimytilus + Septifer + Volsellina + Crenomytilus	Genus	75	N	González-Tizón et al. 2000/WMSDB/PalaeoDB
Mytilidae	Mytilus	Genus	111	Y	González-Tizón et al. 2000/WMSDB/PalaeoDB
Corbiculacea	Cyrenidae	Family	234	N	Lee et al. 1999/WMSDB/PalaeoDB
Corbiculacea	Sphaeriidae	Family	263	Y	Lee et al. 1999/WMSDB/PalaeoDB
Bulinini	Indoplanorbis	Genus	1	N	Goldman & Chrisman 1983/WMSDB/PalaeoDB
Bulinini	Bulinus	Genus	61	Y	Goldman & Chrisman 1983/WMSDB/PalaeoDB
Thiaridae	Tarebia + Thiara	Genus	77	N	Jacob 1959/Jena & Srirama 2017/WMSDB/PalaeoDB
Thiaridae	Melanoides	Genus	98	Y	Jacob 1959/Jena & Srirama 2017/WMSDB/PalaeoDB
Tateidae	Sororipyrgus	Genus	3	N	Soper et al 2016/Zielske et al. 2017/WMSDB/PalaeoDB
Tateidae	Potamopyrgus	Genus	35	Y	Soper et al 2016/Zielske et al. 2017/WMSDB/PalaeoDB
Austrobaileyales	Trimeniaceae	Family	12	N	Stebbins 1950/APG IV 2016/The Plant List/PalaeoDB

Austrobaileyales	Illiciaceae + Schisandraceae	Family	73	Y	Stebbins 1950/APG IV 2016/The Plant List/PalaeoDB
Laurales 1	Monimiaceae	Family	135	N	Stebbins 1950/APG IV 2016/The Plant List/PalaeoDB
Laurales 1	Lauraceae	Family	3028	Y	Stebbins 1950/APG IV 2016/The Plant List/PalaeoDB
Laurales 2	Siparunaceae + Atherospermataceae + Gomortegaceae + Hernandiaceae + Monimiaceae + Lauraceae	Family	3286	N	Stebbins 1950/APG IV 2016/The Plant List/PalaeoDB
Laurales 2	Calycanthaceae	Family	11	Y	Stebbins 1950/APG IV 2016/The Plant List/PalaeoDB
Magnoliales 1	Degeneriaceae+Himantandraceae	Family	3	N	Stebbins 1950/Sauquet & al. 2003/The Plant List/PalaeoDB
Magnoliales 1	Magnoliaceae	Family	251	Y	Stebbins 1950/Sauquet & al. 2003/The Plant List/PalaeoDB
Magnoliales 2	Eupomatiaceae	Family	3	N	Ehrendorfer et al. 1968/Soltis & Soltis 2004/The Plant List/PalaeoDB
Magnoliales 2	Annonaceae	Family	3342	Y	Ehrendorfer et al. 1968/Soltis & Soltis 2004/The Plant List/PalaeoDB
Magnolieae	Michelia	Genus	23	N	Parris et al. 2012/Kim & Suh 2013/The Plant List/PalaeoDB
Magnolieae	Magnolia	Genus	272	Y	Parris et al. 2012/Kim & Suh 2013/The Plant List/PalaeoDB
Canellales	Canellaceae	Family	24	N	Ehrendorfer & Lambrou 2000/The Plant List/PalaeoDB
Canellales	Winteraceae	Family	163	Y	Ehrendorfer & Lambrou 2000/The Plant List/PalaeoDB
Piperaceae	Zippelioideae	Subfamily	7	N	Jose & Sharma 1985/Tucker et al. 1993/The Plant List/PalaeoDB
Piperaceae	Piperoideae	Subfamily	4719	Y	Jose & Sharma 1985/Tucker et al. 1993/The Plant List/PalaeoDB
Chloranthaceae	Sarcandra	Genus	4	N	Ehrendorfer et al. 1968/Eklund et al. 2004/The Plant List/PalaeoDB
Chloranthaceae	Chloranthus	Genus	20	Y	Ehrendorfer et al. 1968/Eklund et al. 2004/The Plant List/PalaeoDB
Basal Eudicots	Buxaceae	Family	123	N	Stebbins 1950/Saarela et al. 2007/The Plant List/PalaeoDB
Basal Eudicots	Trochodendraceae	Family	2	Y	Stebbins 1950/Saarela et al. 2007/The Plant List/PalaeoDB
Proteales	Proteaceae	Family	1323	N	Stebbins 1950/Tree of Life/The Plant List/PalaeoDB
Proteales	Platanaceae	Family	27	Y	Stebbins 1950/Tree of Life/The Plant List/PalaeoDB
Saxifragales	Hamamelidaceae + Paeoniaceae	Genus	143	N	Stebbins 1950/Fishbein et al. 2001/The Plant List/PalaeoDB

Saxifragales	Cercidiphyllaceae	Genus	7	Y	Stebbins 1950/Fishbein et al. 2001/The Plant List/PalaeoDB
Malpighiales	Lacistemataceae	Family	13	N	Stebbins 1950/Wurdack & Davis 2009/The Plant List/PalaeoDB
Malpighiales	Salicaceae	Family	1275	Y	Stebbins 1950/Wurdack & Davis 2009/The Plant List/PalaeoDB
Sapindales	Simaroubaceae	Family	121	N	Stebbins 1950/Buerki et al. 2010/The Plant List/PalaeoDB
Sapindales	Sapindaceae	Family	1759	Y	Stebbins 1950/Buerki et al. 2010/The Plant List/PalaeoDB
Brassicaceae 1	Catolobus	Genus	1	N	Marhold & Lihova 2006/Beilstein 2006/The Plant List/PalaeoDB
Brassicaceae 1	Arabidopsis	Genus	16	Y	Marhold & Lihova 2006/Beilstein 2006/The Plant List/PalaeoDB
Brassicaceae 2	Iodanthus	Genus	2	N	Marhold & Lihova 2006/Beilstein 2006/The Plant List/PalaeoDB
Brassicaceae 2	Cardamine	Genus	236	Y	Marhold & Lihova 2006/Beilstein 2006/The Plant List/PalaeoDB
Brassicaceae 3	Cakile	Genus	7	N	Marhold & Lihova 2006/Beilstein 2006/The Plant List/PalaeoDB
Brassicaceae 3	Brassica	Genus	39	Y	Marhold & Lihova 2006/Beilstein 2006/The Plant List/PalaeoDB
Brassicaceae 4	Dimorphocarpa	Genus	5	N	Marhold & Lihova 2006/Beilstein 2006/The Plant List/PalaeoDB
Brassicaceae 4	Physaria	Genus	107	Y	Marhold & Lihova 2006/Beilstein 2006/The Plant List/PalaeoDB
Brassicaceae 5	Rapistrum + Diplotaxis	Genus	39	N	Marhold & Lihova 2006/Warwick & Sauder 2005/The Plant List/PalaeoDB
Brassicaceae 5	Crambe	Genus	39	Y	Marhold & Lihova 2006/Warwick & Sauder 2005/The Plant List/PalaeoDB
Brassicaceae 6	Rytidocarpus	Genus	1	N	Marhold & Lihova 2006/Beilstein 2006/The Plant List/PalaeoDB
Brassicaceae 6	Moricandia	Genus	8	Y	Marhold & Lihova 2006/Beilstein 2006/The Plant List/PalaeoDB
Brassicaceae 7	Athysanus + Heterodraba	Genus	2	N	Marhold & Lihova 2006/Jordon-Thaden et al. 2010/The Plant List/PalaeoDB
Brassicaceae 7	Draba	Genus	400	Y	Marhold & Lihova 2006/Jordon-Thaden et al. 2010/The Plant List/PalaeoDB
Brassicaceae 8	Barbarea	Genus	29	N	Marhold & Lihova 2006/Huang et al. 2015/The Plant List/PalaeoDB
Brassicaceae 8	Rorippa	Genus	91	Y	Marhold & Lihova 2006/Huang et al. 2015/The Plant List/PalaeoDB
Caricaceae	Jacaratia + Vasconcellea	Genus	13	N	Song et al. 2012/Kyndt et al. 2005/The Plant List/PalaeoDB

Caricaceae	Carica	Genus	1	Y	Song et al. 2012/Kyndt et al. 2005/The Plant List/PalaeoDB
Andropogoneae	Miscanthus	Genus	16	N	Song et al. 2012/Mathews et al. 2002/The Plant List/PalaeoDB
Andropogoneae	Saccharum	Genus	36	Y	Song et al. 2012/Mathews et al. 2002/The Plant List/PalaeoDB
Coffeeae	Calycosiphonia + Argocoffeopsis + Diplospora + Belonophora + Discospermum	Genus	48	N	Song et al. 2012/ Davis et al. 2007/The World Checklist of Rubiaceae/PalaeoDB
Coffeeae	Coffea	Genus	124	Y	Song et al. 2012/Davis et al. 2007/The Plant List/PalaeoDB
Gossypieae	Gossypioides + Kokia	Genus	7	N	Song et al. 2012/Rudges et al. 2004/The Plant List/PalaeoDB
Gossypieae	Gossypium	Genus	54	Y	Song et al. 2012/Rudges et al. 2004/The Plant List/PalaeoDB
Nicotianeae	Anthocercis + Anthotroche + Crenidium + Cyphanthera + Duboisia + Grammosolen + Symonanthus	Genus	30	N	Song et al. 2012/Clarkson et al. 2004/The Plant List/ PalaeoDB
Nicotianeae	Nicotiana	Genus	55	Y	Song et al. 2012/Clarkson et al. 2004/The Plant List/ PalaeoDB
Triticeae	Aegilops	Genus	25	N	Song et al. 2012/Mason-Gamer et al. 2002/The Plant List/ PalaeoDB
Triticeae	Triticum	Genus	28	Y	Song et al. 2012/Mason-Gamer et al. 2002/The Plant List/ PalaeoDB
Musaceae	Ensete	Genus	10	N	Song et al. 2012/The Plant List/ PalaeoDB
Musaceae	Musa	Genus	70	Y	Song et al. 2012/The Plant List/ PalaeoDB
Narcisseae	Sternbergia	Genus	9	N	Song et al. 2012/Meerow et al. 2006/The Plant List/ PalaeoDB
Narcisseae	Narcissus	Genus	116	Y	Song et al. 2012/Meerow et al. 2006/The Plant List/ PalaeoDB
Hemerocallidoideae	Simethis	Genus	1	N	Song et al. 2012/McLay & Bayly 2016/The Plant List/ PalaeoDB
Hemerocallidoideae	Hemerocallis	Genus	19	Y	Song et al. 2012/McLay & Bayly 2016/The Plant List/ PalaeoDB
Solaneae	Jaltomata	Genus	35	N	Song et al. 2012/Olmstead et al. 2008/The Plant List/ PalaeoDB
Solaneae	Solanum	Genus	1199	Y	Song et al. 2012/Olmstead et al. 2008/The Plant List/ PalaeoDB
Araceae	Remusatia + Steudnera	Genus	13	N	Song et al. 2012/Cusimano et al. 2011/The Plant List/ PalaeoDB
Araceae	Colocasia	Genus	8	Y	Song et al. 2012/Cusimano et al. 2011/The Plant List/ PalaeoDB
Allieae	Prototulbaghia + Tulbaghia + Leucocoryneae + Gilliesieae	Genus	230	N	Song et al. 2012/Li et al. 2010/The Plant List/ PalaeoDB
Allieae	Allium	Genus	918	Y	Song et al. 2012/Li et al. 2010/The Plant List/ PalaeoDB
Dioscoreaceae	Rajania	Genus	19	N	Song et al. 2012/Caddick et al. 2002/The Plant List/ PalaeoDB

Dioscoreaceae	Disoscorea	Genus	613	Y	Song et al. 2012/Caddick et al. 2002/The Plant List/ PalaeoDB
Diocleae	Cleobulia + Cymbosema + Dioclea + Macropsychanthus + Bionia + Camptosema + Collaea + Cratylia + Galactia + Lackeya + Neorudolphia + Rhodopis	Genus	222	N	Song et al. 2012/Wojciechowski et al. 2004/The Plant List/ PalaeoDB
Diocleae	Canavalia	Genus	70	Y	Song et al. 2012/Wojciechowski et al. 2004/The Plant List/ PalaeoDB
Primulaceae	Dionysia	Genus	54	N	Song et al. 2012/Martins et al. 2003/The Plant List/ PalaeoDB
Primulaceae	Primula	Genus	392	Y	Song et al. 2012/Martins et al. 2003/The Plant List/ PalaeoDB
Senecioneae	Chersodoma	Genus	9	N	Leitch & Leitch 2008/Pelser et al. 2007/The Plant List/ PalaeoDB
Senecioneae	Senecio	Genus	1587	Y	Leitch & Leitch 2008/Pelser et al. 2007/The Plant List/ PalaeoDB
Tripsacinae	Tripsacum	Genus	14	N	Leitch & Leitch 2008/Hodkinson et al. 2002/The Plant List/ PalaeoDB
Tripsacinae	Zea	Genus	6	Y	Leitch & Leitch 2008/Hodkinson et al. 2002/The Plant List/ PalaeoDB
Agavoideae	Beschorneria + Furcraea	Genus	31	N	Leitch & Leitch 2008/McKain et al. 2016. 2005/The Plant List/ PalaeoDB
Agavoideae	Agave	Genus	200	Y	Leitch & Leitch 2008/ McKain et al. 2016. /The Plant List/ PalaeoDB
Vaccinieae	Orthaea+Notopora	Genus	39	N	Wood et al. 2009/Kron et al. 2002/The Plant List/PalaeoDB
Vaccinieae	Vaccinium	Genus	223	Y	Wood et al. 2009/Kron et al. 2002/The Plant List/PalaeoDB
Crassulaceae	Monanthes	Genus	12	N	Wood et al. 2009/Mort et. al 2001/The Plant List/PalaeoDB
Crassulaceae	Aichryson	Genus	18	Y	Wood et al. 2009/Mort et. al 2001/The Plant List/PalaeoDB
Gesneriaceae	Koellikeria+Gloxinia+Diastema+Monopyle+Kohleria+Pearcea+Phinaea+Moussonia+Smithiantha+Eucodonia+Niphaea	Genus	130	N	Wood et al. 2009/Zimmer et al. 2002/The Plant List/PalaeoDB
Gesneriaceae	Achimenes	Genus	26	Y	Wood et al. 2009/Zimmer et al. 2002/The Plant List/PalaeoDB
Primulaceae	Primula	Genus	392	N	Wood et al. 2009/Martins et al. 2003/The Plant List/PalaeoDB
Primulaceae	Dodecatheon	Genus	15	Y	Wood et al. 2009/Martins et al. 2003/The Plant List/PalaeoDB
Lilioideae	Lloydia	Genus	7	N	Wood et al. 2009/Ronsted et al. 2005/The Plant List/PalaeoDB

Lilioideae	Gagea	Genus	209	Y	Wood et al. 2009/Ronsted et al. 2005/The Plant List/PalaeoDB
Plantaginaceae	Erinus	Genus	2	N	Wood et al. 2009/Albach et al. 2005/The Plant List/PalaeoDB
Plantaginaceae	Digitalis+Isoplexis	Genus	26	Y	Wood et al. 2009/Albach et al. 2005/The Plant List/PalaeoDB
Mentheae	Cyclotrichium	Genus	9	N	Wood et al. 2009/Drew & Sytsma 2012/The Plant List/PalaeoDB
Mentheae	Mentha	Genus	42	Y	Wood et al. 2009/Drew & Sytsma 2012/The Plant List/PalaeoDB
Triticeae	Elymus	Genus	234	N	Wood et al. 2009/Monte et al. 1993/The Plant List/PalaeoDB
Triticeae	Psathyrostachys	Genus	10	Y	Wood et al. 2009/Monte et al. 1993/The Plant List/PalaeoDB
Sileneae	Lychnis	Genus	14	N	Wood et al. 2009/Oxelman et al. 1997/The Plant List/PalaeoDB
Sileneae	Silene	Genus	488	Y	Wood et al. 2009/Oxelman et al. 1997/The Plant List/PalaeoDB
Apiaceae	Cryptotaenia+Oxypolis+Sium+Cicuta+ Oenanthe	Genus	58	N	Wood et al. 2009/Downie et al. 2000/The Plant List/PalaeoDB
Apiaceae	Perideridia	Genus	15	Y	Wood et al. 2009/Downie et al. 2000/The Plant List/PalaeoDB
Heliantheae	Baeriopsis+Amblyopappus	Genus	2	N	Wood et al. 2009/Baldwin & Wessa 2000/The Plant List/PalaeoDB
Heliantheae	Lasthenia	Genus	19	Y	Wood et al. 2009/Baldwin & Wessa 2000/The Plant List/PalaeoDB
Arethuseae	Arethusa+Eleorchis	Genus	2	N	Wood et al. 2009/Goldman et al. 2001/The Plant List/PalaeoDB
Arethuseae	Calopogon	Genus	5	Y	Wood et al. 2009/Goldman et al. 2001/The Plant List/PalaeoDB
Microseridinae	Uropappus	Genus	3	N	Wood et al. 2009/ Lohwasser et al. 2004/The Plant List/PalaeoDB
Microseridinae	Microseris	Genus	43	Y	Wood et al. 2009/ Lohwasser et al. 2004/The Plant List/PalaeoDB
Brassicaceae 1	Catalobus	Genus	1	N	Wood et al. 2009/Beilstein et al. 2006/The Plant List/PalaeoDB
Brassicaceae 1	Capsella	Genus	9	Y	Wood et al. 2009/Beilstein et al. 2006/The Plant List/PalaeoDB
Brassicaceae 2	Selenia	Genus	5	N	Wood et al. 2009/Beilstein et al. 2006/The Plant List/PalaeoDB
Brassicaceae 2	Leavenworthia	Genus	9	Y	Wood et al. 2009/Beilstein et al. 2006/The Plant List/PalaeoDB
Spermacoceae	Stenaria	Genus	6	N	Wood et al. 2009/Karehed et al. 2008/The Plant List/PalaeoDB
Spermacoceae	Houstonia	Genus	23	Y	Wood et al. 2009/Karehed et al. 2008/The Plant List/PalaeoDB

Phrymaceae	Glossostigma+Peplidium	Genus	16	N	Wood et al. 2009/Beardsley & Olmstead 2002/The Plant List/PalaeoDB
Phrymaceae	Mimulus	Genus	155	Y	Wood et al. 2009/Beardsley & Olmstead 2002/The Plant List/PalaeoDB
Veroniceae	Paederota	Genus	7	N	Wood et al. 2009/Albach et al. 2004/The Plant List/PalaeoDB
Veroniceae	Veronica	Genus	198	Y	Wood et al. 2009/Albach et al. 2004/The Plant List/PalaeoDB
Onagreae	Camissonia	Genus	23	N	Wood et al. 2009/Levin et al. 2004/The Plant List/PalaeoDB
Onagreae	Gaura	Genus	90	Y	Wood et al. 2009/Levin et al. 2004/The Plant List/PalaeoDB
Sorghinae	Chrysopogon+Microstegium+Apluda+ Sorghastrum	Genus	93	N	Wood et al. 2009/Liu et al. 2014/The Plant List/PalaeoDB
Sorghinae	Sorghum	Genus	31	Y	Wood et al. 2009/Liu et al. 2014/The Plant List/PalaeoDB
Anthemideae	Anacyclus+Matricaria	Genus	37	N	Wood et al. 2009/Watson et al. 2000/The Plant List/PalaeoDB
Anthemideae	Achillea	Genus	151	Y	Wood et al. 2009/Watson et al. 2000/The Plant List/PalaeoDB
Coreopsideae	Bidens	Genus	249	N	Wood et al. 2009/Kimbal & Crawford 2004/The Plant List/PalaeoDB
Coreopsideae	Coreopsis	Genus	100	Y	Wood et al. 2009/Kimbal & Crawford 2004/The Plant List/PalaeoDB
Hypochaeridinae	Scorzoneroides	Genus	25	N	Wood et al. 2009/Enke et al. 2012/The Plant List/PalaeoDB
Hypochaeridinae	Hypochaeris+Leontodon+Helminthotheca+Picris	Genus	230	Y	Wood et al. 2009/Enke et al. 2012/The Plant List/PalaeoDB
Machaerantherinae	Oonopsis	Genus	4	N	Wood et al. 2009/Morgan et al. 2009/The Plant List/PalaeoDB
Machaerantherinae	Machaeranthera	Genus	27	Y	Wood et al. 2009/Morgan et al. 2009/The Plant List/PalaeoDB
Campanulaceae	Trachelium	Genus	3	N	Wood et al. 2009/Park et al. 2006/The Plant List/PalaeoDB
Campanulaceae	Campanula sect. Isophylla	Genus	441	Y	Wood et al. 2009/Park et al. 2006/The Plant List/PalaeoDB
Ehretioideae	Bourreria	Genus	56	N	Wood et al. 2009/Moore et al. 2006/The Plant List/PalaeoDB
Ehretioideae	Tiquilia	Genus	28	Y	Wood et al. 2009/Moore et al. 2006/The Plant List/PalaeoDB
Hydrophylloideae	Romanzoffia	Genus	5	N	Wood et al. 2009/Walden et al. 2014/The Plant List/PalaeoDB
Hydrophylloideae	Phacelia	Genus	186	Y	Wood et al. 2009/Walden et al. 2014/The Plant List/PalaeoDB
Adoxaceae	Sambucus	Genus	30	N	Wood et al. 2009/Donoghue et al. 2004/The Plant List/Huang et al. 2012

Adoxaceae	Viburnum	Genus	169	Y	Wood et al. 2009/Donoghue et al. 2004/The Plant List/PalaeoDB
Actinidiaceae	Saurauia+Clematoclethra	Genus	103	N	Wood et al. 2009/Chat et al. 2004/The Plant List/PalaeoDB
Actinidiaceae	Actinidia	Genus	76	Y	Wood et al. 2009/Chat et al. 2004/The Plant List/PalaeoDB
Polemoniaceae	Gilia+Navarettia	Genus	70	N	Wood et al. 2009/Prather et al. 2000/The Plant List/PalaeoDB
Polemoniaceae	Collomia	Genus	15	Y	Wood et al. 2009/Prather et al. 2000/The Plant List/PalaeoDB
Geraniaceae	Erodium+Geranium+Monsonia+Sarcocaulon	Genus	582	N	Wood et al. 2009/Price & Palmer 1993/The Plant List/PalaeoDB
Geraniaceae	Pelargonium	Genus	1697	Y	Wood et al. 2009/Price & Palmer 1993/The Plant List/PalaeoDB
Orobanchaceae	Epifagus+Conopholis+Boschniakia	Genus	7	N	Wood et al. 2009/Bennett & Mathews 2006/The Plant List/PalaeoDB
Orobanchaceae	Orobanche	Genus	119	Y	Wood et al. 2009/Bennett & Mathews 2006/The Plant List/PalaeoDB
Cheloneae	Chelone+Nothochelone	Genus	6	N	Wood et al. 2009/Wolfe et al. 1997/The Plant List/PalaeoDB
Cheloneae	Penstemon	Genus	301	Y	Wood et al. 2009/Wolfe et al. 1997/The Plant List/PalaeoDB
Antirrhineae	Neogaerrhinum +Sairocarpus+Mohavea+Galvezia	Genus	21	N	Wood et al. 2009/Vargas et al. 2004/The Plant List/PalaeoDB
Antirrhineae	Antirrhinum	Genus	21	Y	Wood et al. 2009/Vargas et al. 2004/The Plant List/PalaeoDB
Physalinae	Margaranthus	Genus	2	N	Wood et al. 2009/Whitson & Manos 2005/The Plant List/PalaeoDB
Physalinae	Physalis	Genus	126	Y	Wood et al. 2009/Whitson & Manos 2005/The Plant List/PalaeoDB
Aristolochioideae	Pararistolochia	Genus	10	N	Wood et al. 2009/Wanke et al. 2006/The Plant List/PalaeoDB
Aristolochioideae	Aristolochia	Genus	487	Y	Wood et al. 2009/Wanke et al. 2006/The Plant List/PalaeoDB
Montiaceae	Lewisia	Genus	17	N	Wood et al. 2009/Ogburn & Edwards 2015/The Plant List/PalaeoDB
Montiaceae	Claytonia+Montia+Neopaxia	Genus	35	Y	Wood et al. 2009/Ogburn & Edwards 2015/The Plant List/PalaeoDB
Gunneraceae	Myrothamnus	Genus	2	N	Wood et al. 2009/De Craene & Wanntorp 2006/The Plant List/PalaeoDB
Gunneraceae	Gunnera	Genus	69	Y	Wood et al. 2009/De Craene & Wanntorp 2006/The Plant List/PalaeoDB
Polemoniaceae	Mitella+Conimitella+Heuchera+Tiarella+Elmera+Tolmiea+Lithophragma+Bensoniella	Genus	96	N	Wood et al. 2009/Johnson & Soltis 1995/The Plant List/PalaeoDB
Polemoniaceae	Saxifraga	Genus	450	Y	Wood et al. 2009/Johnson & Soltis 1995/The Plant List/PalaeoDB

Alismatales	Scheuchzeriaceae+Juncaginaceae+Posidoniaceae+Cymodoceaceae+Ruppiaceae	Genus	90	N	Wood et al. 2009/Iles et al. 2013/The Plant List/PalaeoDB
Alismatales	Aponogetonaceae	Genus	58	Y	Wood et al. 2009/Iles et al. 2013/The Plant List/PalaeoDB
Arisaemateae	Pinellia	Genus	9	N	Wood et al. 2009/Cabrera et al. 2008/The Plant List/PalaeoDB
Arisaemateae	Arisaema	Genus	180	Y	Wood et al. 2009/Cabrera et al. 2008/The Plant List/PalaeoDB
Lemnoideae	Spirodela	Genus	4	N	Wood et al. 2009/Wang et al. 2011/The Plant List/PalaeoDB
Lemnoideae	Lemna+Wolffia+Wolffiella	Genus	35	Y	Wood et al. 2009/Wang et al. 2011/The Plant List/PalaeoDB
Burmanniaceae	Dioscorea	Genus	614	N	Wood et al. 2009/Merckx et al. 2006/The Plant List/PalaeoDB
Burmanniaceae	Burmannia+Gymnosiphon+Apteria+Cymbocarpa+Hexapterella+Dictyostega	Genus	92	Y	Wood et al. 2009/Merckx et al. 2006/The Plant List/PalaeoDB
Trilliaceae	Pseudotrillium	Genus	1	N	Wood et al. 2009/Farmer 2006/The Plant List/PalaeoDB
Trilliaceae	Trillium+Paris	Genus	77	Y	Wood et al. 2009/Farmer 2006/The Plant List/PalaeoDB
Oryzinae	Leersia	Genus	18	N	Wood et al. 2009/Guo & Ge 2005/The Plant List/PalaeoDB
Oryzinae	Oryza	Genus	18	Y	Wood et al. 2009/Guo & Ge 2005/The Plant List/PalaeoDB
Lepidieae	Iberis+Capsella	Genus	38	N	Wood et al. 2009/Zunk et al. 1999/The Plant List/PalaeoDB
Lepidieae	Lepidium	Genus	234	Y	Wood et al. 2009/Zunk et al. 1999/The Plant List/PalaeoDB
Cucurbitaceae	Muellerargia	Genus	1	N	Wood et al. 2009/Schaefer et al. 2008/The Plant List/PalaeoDB
Cucurbitaceae	Cucumis	Genus	52	Y	Wood et al. 2009/Schaefer et al. 2008/The Plant List/PalaeoDB
Fabeae	Pisum	Genus	7	N	Wood et al. 2009/Schaefer et al. 2012/The Plant List/PalaeoDB
Fabeae	Lathyrus	Genus	186	Y	Wood et al. 2009/Schaefer et al. 2012/The Plant List/PalaeoDB
Betulaceae	Alnus	Genus	46	N	Wood et al. 2009/Chen et al. 1999/The Plant List/PalaeoDB
Betulaceae	Betula	Genus	121	Y	Wood et al. 2009/Chen et al. 1999/The Plant List/PalaeoDB
Malvoideae	Nototriche	Genus	94	N	Wood et al. 2009/Tate et al. 2005/The Plant List/PalaeoDB
Malvoideae	Tarasa	Genus	27	Y	Wood et al. 2009/Tate et al. 2005/The Plant List/PalaeoDB
Lythraceae	Woodfordia	Genus	2	N	Wood et al. 2009/Graham et al. 2005/The Plant List/PalaeoDB

Lythraceae	Cuphea	Genus	280	Y	Wood et al. 2009/Graham et al. 2005/The Plant List/PalaeoDB
Circaeeae	Circaea	Genus	15	N	Wood et al. 2009/Berry et al. 2004/The Plant List/PalaeoDB
Circaeeae	Fuschia	Genus	110	Y	Wood et al. 2009/Berry et al. 2004/The Plant List/PalaeoDB
Rosoideae	Waldsteinia	Genus	4	N	Wood et al. 2009/Eriksson et al. 2003/The Plant List/PalaeoDB
Rosoideae	Geum/allies	Genus	35	Y	Wood et al. 2009/Eriksson et al. 2003/The Plant List/PalaeoDB
Selineae	Lomatium	Genus	87	N	Wood et al. 2009/Spalik et al. 2004/The Plant List/PalaeoDB
Selineae	Angelica	Genus	116	Y	Wood et al. 2009/Spalik et al. 2004/The Plant List/PalaeoDB
Gnaphalieae	Leontopodium	Genus	61	N	Wood et al. 2009/Bayer et al. 1996/The Plant List/PalaeoDB
Gnaphalieae	Antennaria	Genus	61	Y	Wood et al. 2009/Bayer et al. 1996/The Plant List/PalaeoDB
Apiaceae	Apiaceae	Genus	3257	N	Wood et al. 2009/Neves et al. 2004/The Plant List/PalaeoDB
Apiaceae	Bupleurum	Genus	208	Y	Wood et al. 2009/Neves et al. 2004/The Plant List/PalaeoDB
Asteraceae	Calotis	Genus	27	N	Wood et al. 2009/Noyes & Rieseberg 1999/The Plant List/PalaeoDB
Asteraceae	Aster	Genus	234	Y	Wood et al. 2009/Noyes & Rieseberg 1999/The Plant List/PalaeoDB
Senecioneae	Senecio+Lopholaena+Blennosperma+ Syneilesis	Genus	1613	N	Wood et al. 2009/Fernandez et al. 2001/The Plant List/PalaeoDB
Senecioneae	Doronicum	Genus	39	Y	Wood et al. 2009/Fernandez et al. 2001/The Plant List/PalaeoDB
Ericaceae	Bryanthus+Empetrum	Genus	4	N	Wood et al. 2009/Kron & King 1996/The Plant List/PalaeoDB
Ericaceae	Kalmia	Genus	10	Y	Wood et al. 2009/Kron & King 1996/The Plant List/PalaeoDB
Apiaceae	Eyngium	Genus	250	N	Wood et al. 2009/Calvino & Downie 2007/The Plant List/PalaeoDB
Apiaceae	Sanicula	Genus	44	Y	Wood et al. 2009/Calvino & Downie 2007/The Plant List/PalaeoDB
Aralieae	Aralia	Genus	74	N	Wood et al. 2009/Wen et al. 2001/The Plant List/PalaeoDB
Aralieae	Panax	Genus	12	Y	Wood et al. 2009/Wen et al. 2001/The Plant List/PalaeoDB
Galantheae	Leucojum	Genus	2	N	Wood et al. 2009/Meerow et al. 2006/The Plant List/PalaeoDB
Galantheae	Galanthus	Genus	21	Y	Wood et al. 2009/Meerow et al. 2006/The Plant List/PalaeoDB

Amaryllidaceae	Habranthus	Genus	83	N	Wood et al. 2009/Meerow et al. 2000/The Plant List/PalaeoDB
Amaryllidaceae	Zephyranthes	Genus	88	Y	Wood et al. 2009/Meerow et al. 2001/The Plant List/PalaeoDB
Aralioideae	Trevesia	Genus	11	N	Wood et al. 2009/Meerow et al. 2001/The Plant List/PalaeoDB
Aralioideae	Hedera	Genus	18	Y	Wood et al. 2009/Meerow et al. 2001/The Plant List/PalaeoDB
Asclepiadoideae	Stapelia	Genus	56	N	Wood et al. 2009/Rapini et al. 2003/The Plant List/PalaeoDB
Asclepiadoideae	Ceropegia	Genus	217	Y	Wood et al. 2009/Rapini et al. 2003/The Plant List/PalaeoDB
Anthemideae	Leucanthemella+Eumorphia+Arctanthemum+Crossostephium+Ajania+Tripleurospermum	Genus	87	N	Wood et al. 2009/Watson et al. 2000/The Plant List/PalaeoDB
Anthemideae	Artemisia	Genus	481	Y	Wood et al. 2009/Watson et al. 2000/The Plant List/PalaeoDB
Boraginaceae	Plagiobothrys	Genus	79	N	Wood et al. 2009/Huang et al. 2013/The Plant List/PalaeoDB
Boraginaceae	Amsinckia	Genus	14	Y	Wood et al. 2009/Huang et al. 2013/The Plant List/PalaeoDB
Plantaginaceae	Streptocarpus	Genus	134	N	Wood et al. 2009/Albach et al. 2005/The Plant List/PalaeoDB
Plantaginaceae	Callitriche	Genus	63	Y	Wood et al. 2009/Albach et al. 2005/The Plant List/PalaeoDB
Lobelioideae	Clermontia	Genus	24	N	Wood et al. 2009/Cosner et al. 1994/The Plant List/PalaeoDB
Lobelioideae	Lobelia	Genus	414	Y	Wood et al. 2009/Cosner et al. 1994/The Plant List/PalaeoDB
Caryophyllaceae	Arenaria	Genus	273	N	Wood et al. 2009/Fior & Karis et al. 2007/The Plant List/PalaeoDB
Caryophyllaceae	Moehringia	Genus	30	Y	Wood et al. 2009/Fior & Karis et al. 2007/The Plant List/PalaeoDB
Betoideae	Hablitzia+Aphanisma+Oreobliton+Patellifolia	Genus	4	N	Wood et al. 2009/Kadereit et al. 2006/The Plant List/PalaeoDB
Betoideae	Beta	Genus	9	Y	Wood et al. 2009/Kadereit et al. 2006/The Plant List/PalaeoDB
Rhodoreae	Ledum	Genus	6	N	Wood et al. 2009/Kron & Judd 1990/The Plant List/PalaeoDB
Rhodoreae	Rhododendron	Genus	641	Y	Wood et al. 2009/Kron & Judd 1990/The Plant List/PalaeoDB
Dalbergieae	Arachis	Genus	81	N	Wood et al. 2009/Saslis-Lagoudakis et al. 2008/The Plant List/PalaeoDB
Dalbergieae	Stylosanthes	Genus	46	Y	Wood et al. 2009/Saslis-Lagoudakis et al. 2008/The Plant List/PalaeoDB
Chironieae	Chironia+Orphium	Genus	26	N	Wood et al. 2009/Mansion et al. 2005/The Plant List/PalaeoDB

Chironieae	Centaurium	Genus	31	Y	Wood et al. 2009/Mansion et al. 2005/The Plant List/PalaeoDB
Hamamelidaceae	Loropetalum	Genus	3	N	Wood et al. 2009/Shi et al. 1998/The Plant List/PalaeoDB
Hamamelidaceae	Corylopsis	Genus	27	Y	Wood et al. 2009/Shi et al. 1998/The Plant List/PalaeoDB
Iridaceae	Sparaxis	Genus	15	N	Wood et al. 2009/Goldblatt et al. 2008/The Plant List/PalaeoDB
Iridaceae	Iris	Genus	362	Y	Wood et al. 2009/Goldblatt et al. 2008/The Plant List/PalaeoDB
Lamiaceae	Pycnanthes+Blephilia	Genus	6	N	Wood et al. 2009/Prather et al. 2002/The Plant List/PalaeoDB
Lamiaceae	Monarda	Genus	22	Y	Wood et al. 2009/Prather et al. 2002/The Plant List/PalaeoDB
Asparagoideae	Hemiphylacus	Genus	5	N	Wood et al. 2009/Chase et al. 2009/The Plant List/PalaeoDB
Asparagoideae	Asparagus	Genus	211	Y	Wood et al. 2009/Chase et al. 2009/The Plant List/PalaeoDB
Sanguisorbinae	Cliffortia	Genus	105	N	Wood et al. 2009/Chung et al. 2010/The Plant List/PalaeoDB
Sanguisorbinae	Sanguisorba	Genus	26	Y	Wood et al. 2009/Chung et al. 2010/The Plant List/PalaeoDB
Vellinae	Euzomodendron	Genus	3	N	Wood et al. 2009/Crespo et al. 2000/The Plant List/PalaeoDB
Vellinae	Vella	Genus	7	Y	Wood et al. 2009/Crespo et al. 2000/The Plant List/PalaeoDB
Mercurialinae	Discoclaoxylon+Lobanilia+Micrococca +Erythrococca+Claoxylon	Genus	178	N	Wood et al. 2009/Wurdack et al. 2005/The Plant List/PalaeoDB
Mercurialinae	Mercurialis	Genus	14	Y	Wood et al. 2009/Wurdack et al. 2005/The Plant List/PalaeoDB
Poeae	Helictotrichon	Genus	90	N	Wood et al. 2009/Soreng et al. 2007/The Plant List/PalaeoDB
Poeae	Avena	Genus	22	Y	Wood et al. 2009/Soreng et al. 2007/The Plant List/PalaeoDB
Coriariaceae	Francoa+Geranium	Genus	418	N	Wood et al. 2009/Hoot et al. 1999/The Plant List/PalaeoDB
Coriariaceae	Coriaria	Genus	16	Y	Wood et al. 2009/Hoot et al. 1999/The Plant List/PalaeoDB
Pooideae	Phalaris	Genus	19	N	Wood et al. 2009/ Hsiao et al. 1995/The Plant List/PalaeoDB
Pooideae	Briza	Genus	22	Y	Wood et al. 2009/ Hsiao et al. 1995/The Plant List/PalaeoDB
Medeoloideae	Medeola	Genus	1	N	Wood et al. 2009/Fay et al. 2006/The Plant List/PalaeoDB

Medeoloideae	Clintonia	Genus	5	Y	Wood et al. 2009/Fay et al. 2006/The Plant List/PalaeoDB
Gnaphalieae	Helichrysum	Genus	506	N	Wood et al. 2009/Smissen et al. 2004/The Plant List/PalaeoDB
Gnaphalieae	Raoulia	Genus	26	Y	Wood et al. 2009/Smissen et al. 2004/The Plant List/PalaeoDB
Didiereaceae	Decarya+Didierea	Genus	1	N	Wood et al. 2009/Applequist 1999/The Plant List/PalaeoDB
Didiereaceae	Alluaudia	Genus	6	Y	Wood et al. 2009/Applequist 1999/The Plant List/PalaeoDB
Cynareae	Carduncellus	Genus	4	N	Wood et al. 2009/Vilatersana et al. 2000/The Plant List/PalaeoDB
Cynareae	Carthamus	Genus	48	Y	Wood et al. 2009/Vilatersana et al. 2000/The Plant List/PalaeoDB
Gnetophytes	Gnetum	Genus	42	N	Khoshoo 1959/Hasebe et al. 1992/The Plant List/PalaeoDB
Gnetophytes	Ephedra	Genus	70	Y	Khoshoo 1959/Hasebe et al. 1992/The Plant List/PalaeoDB
Sequoioideae	Metasequoia	Genus	5	N	Khoshoo 1959/Yang et al. 2012/The Plant List/PalaeoDB
Sequoioideae	Sequoia	Genus	6	Y	Khoshoo 1959/Yang et al. 2012/The Plant List/PalaeoDB
Callitroideae	Diselma	Genus	2	N	Scott et al. 2016/Yang et al. 2012/The Plant List
Callitroideae	Fitzroya	Genus	2	Y	Scott et al. 2016/Yang et al. 2012/The Plant List
Cupressoideae	Xanthocyparis	Genus	2	N	Khoshoo 1959/Yang et al. 2012/The Plant List/PalaeoDB
Cupressoideae	Cupressus+Juniperus	Genus	95	Y	Khoshoo 1959/Yang et al. 2012/Adams 2004/PalaeoDB
Podocarpaceae 1	Falcatifolium	Genus	7	N	Grant 1976/Biffin et al. 2010/The Plant List/PalaeoDB
Podocarpaceae 1	Dacrydium	Genus	28	Y	Grant 1976/Biffin et al. 2010/The Plant List/PalaeoDB
Podocarpaceae 2	Nageia + Afrocarpus + Retrophyllum	Genus	17	N	Grant 1976/Biffin et al. 2010/The Plant List/PalaeoDB
Podocarpaceae 2	Podocarpus	Genus	120	Y	Grant 1976/Biffin et al. 2010/The Plant List/PalaeoDB
Polypodiales	Hemidictyaceae	Genus	1	N	Wood et al. 2009/Rothfels et al. 2012/The Plant List/PalaeoDB
Polypodiales	Aspleniaceae	Genus	517	Y	Wood et al. 2009/Rothfels et al. 2013/The Plant List/PalaeoDB
Blechnaceae	Woodwardia	Genus	27	N	Wood et al. 2009/Gasper et al. 2016/The Plant List/PalaeoDB
Blechnaceae	Blechnum	Genus	148	Y	Wood et al. 2009/Gasper et al. 2016/The Plant List/PalaeoDB

Cyatheaceae	Alsophila	Genus	71	N	Wood et al. 2009/Hill et al. 2003/The Plant List/PalaeoDB
Cyatheaceae	Cyathea	Genus	320	Y	Wood et al. 2009/ Hill et al. 2003/The Plant List/PalaeoDB
Dennstaedtiaceae 1	Leptolepia	Genus	1	N	Wood et al. 2009/Wolf 1995/The Plant List/PalaeoDB
Dennstaedtiaceae 1	Dennstaedtia + Microlepia	Genus	123	Y	Wood et al. 2009/Wolf 1995/The Plant List/PalaeoDB
Dennstaedtiaceae 2	Saccoloma + Paesia + Blotiella + Histiopteris	Genus	34	N	Wood et al. 2009/Wolf 1995/The Plant List/PalaeoDB
Dennstaedtiaceae 2	Hypolepis	Genus	52	Y	Wood et al. 2009/Wolf 1995/The Plant List/PalaeoDB
Dennstaedtiaceae 3	Odontosoria	Genus	14	N	Wood et al. 2009/Lehtonen et al. 2010/The Plant List/PalaeoDB
Dennstaedtiaceae 3	Sphenomeris	Genus	8	Y	Wood et al. 2009/Lehtonen et al. 2010/The Plant List/PalaeoDB
Dryopteridaceae 1	Leptorumohra + Phanerophlebiopis + Lithostegia	Genus	15	N	Wood et al. 2009/Liu et al. 2007/The Plant List/PalaeoDB
Dryopteridaceae 1	Arachniodes	Genus	138	Y	Wood et al. 2009/Liu et al. 2007/The Plant List/PalaeoDB
Physematieae	Pseudocystopteris	Genus	7	N	Wood et al. 2009/Sano et al. 2000/The Plant List/PalaeoDB
Physematieae	Athyrium	Genus	216	Y	Wood et al. 2009/Sano et al. 2000/The Plant List/PalaeoDB
Dryopteridaceae 2	Cyrtogonellum	Genus	8	N	Wood et al. 2009/Liu et al. 2007/The Plant List/PalaeoDB
Dryopteridaceae 2	Cyrtomium	Genus	43	Y	Wood et al. 2009/Liu et al. 2007/The Plant List/PalaeoDB
Cystopteridaceae	Acystopteris	Genus	3	N	Wood et al. 2009/Rothfels et al. 2013/The Plant List/PalaeoDB
Cystopteridaceae	Cystopteris + Gymnocarpium	Genus	35	Y	Wood et al. 2009/Rothfels et al. 2013/The Plant List/PalaeoDB
Athyriaceae	Anisocampium + Cornopteris	Genus	18	N	Wood et al. 2009/Liu et al. 2011/The Plant List/PalaeoDB
Athyriaceae	Diplazium	Genus	211	Y	Wood et al. 2009/Liu et al. 2011/The Plant List/PalaeoDB
Dryopteridaceae 3	Acrorumohra + Peranema + Diacalpe + Acrophorus	Genus	26	N	Wood et al. 2009/Liu et al. 2007/The Plant List/PalaeoDB
Dryopteridaceae 3	Dryopteris	Genus	305	Y	Wood et al. 2009/Liu et al. 2007/The Plant List/PalaeoDB
Elaphoglossoideae	Megalastrum	Genus	55	N	Wood et al. 2009/Liu et al. 2007/The Plant List/PalaeoDB
Elaphoglossoideae	Lastreopsis	Genus	31	Y	Wood et al. 2009/Liu et al. 2007/The Plant List/PalaeoDB
Dryopteridaceae 4	Cyrtogonellum	Genus	8	N	Wood et al. 2009/Liu et al. 2007/The Plant List/PalaeoDB

Dryopteridaceae 4	Polystichum	Genus	276	Y	Wood et al. 2009/Liu et al. 2007/The Plant List/PalaeoDB
Dryopteridaceae 5	Megalastrum	Genus	55	N	Wood et al. 2009/Liu et al. 2007/The Plant List/PalaeoDB
Dryopteridaceae 5	Rumohra	Genus	5	Y	Wood et al. 2009/Liu et al. 2007/The Plant List/PalaeoDB
Dryopteridaceae 6	Prosaptia	Genus	3	N	Wood et al. 2009/Liu et al. 2007/The Plant List/PalaeoDB
Dryopteridaceae 6	Tectaria	Genus	195	Y	Wood et al. 2009/Liu et al. 2007/The Plant List/PalaeoDB
Dryopteridaceae 7	Cheilanthopsis + Peranema	Genus	5	N	Wood et al. 2009/Shao et al. 2015/The Plant List/PalaeoDB
Dryopteridaceae 7	Woodsia	Genus	43	Y	Wood et al. 2009/Shao et al. 2015/The Plant List/PalaeoDB
Pteridophyta	Psilotopsida	Genus	117	N	Wood et al. 2009/Rothwell & Nixon 2006/The Plant List/PalaeoDB
Pteridophyta	Equisetaceae + Marattiales + Polypodiopsida	Genus	793	Y	Wood et al. 2009/Rothwell & Nixon 2006/The Plant List/PalaeoDB
Gleicheniaceae 1	Gleichenella	Genus	1	N	Wood et al. 2009/Rothwell & Nixon 2006/The Plant List/PalaeoDB
Gleicheniaceae 1	Dicranopteris	Genus	20	Y	Wood et al. 2009/Perrie et al. 2007/The Plant List/PalaeoDB
Gleicheniaceae 2	Stromatopteris	Genus	1	N	Wood et al. 2009/Perrie et al. 2007/The Plant List/PalaeoDB
Gleicheniaceae 2	Gleichenia	Genus	18	Y	Wood et al. 2009/Perrie et al. 2007/The Plant List/PalaeoDB
Gleicheniaceae 3	Stromatopteris	Genus	1	N	Wood et al. 2009/Perrie et al. 2007/The Plant List/PalaeoDB
Gleicheniaceae 3	Sticherus	Genus	74	Y	Wood et al. 2009/Perrie et al. 2007/The Plant List/PalaeoDB
Grammitidaceae 1	Prosaptia	Genus	3	N	Wood et al. 2009/Ranker et al. 2004/The Plant List/PalaeoDB
Grammitidaceae 1	Ctenopteris	Genus	22	Y	Wood et al. 2009/Ranker et al. 2004/The Plant List/PalaeoDB
Grammitidaceae 2	Themelium	Genus	1	N	Wood et al. 2009/Ranker et al. 2004/The Plant List/PalaeoDB
Grammitidaceae 2	Xiphopteris	Genus	13	Y	Wood et al. 2009/Ranker et al. 2004/The Plant List/PalaeoDB
Hymenophyllaceae 1	Pachychaetum	Genus	10	N	Wood et al. 2009/Ebihara et al. 2006/The Plant List/PalaeoDB
Hymenophyllaceae 1	Cephalomanes	Genus	12	Y	Wood et al. 2009/Ebihara et al. 2006/The Plant List/PalaeoDB
Hymenophyllaceae 2	Crepidomanes	Genus	32	N	Wood et al. 2009/Pryer et al. 2001/The Plant List/PalaeoDB
Hymenophyllaceae 2	Gonocormus	Genus	2	Y	Wood et al. 2009/Pryer et al. 2001/The Plant List/PalaeoDB

Hymenophyllaceae 3	Didymoglossum + Trichomanes	Genus	139	N	Wood et al. 2009/Pryer et al. 2001/The Plant List/PalaeoDB
Hymenophyllaceae 3	Abrodictyum	Genus	10	Y	Wood et al. 2009/Pryer et al. 2001/The Plant List/PalaeoDB
Hymenophyllaceae 4	Hymenophyllum	Genus	172	N	Wood et al. 2009/Pryer et al. 2001/The Plant List/PalaeoDB
Hymenophyllaceae 4	Sphaerocionium	Genus	10	Y	Wood et al. 2009/Pryer et al. 2001/The Plant List/PalaeoDB
Lycopodiophyta	Lycopodiopsida	Genus	475	N	Wood et al. 2009/The Plant List/PalaeoDB
Lycopodiophyta	Isoetopsida	Genus	1008	Y	Wood et al. 2009/The Plant List/PalaeoDB
Elaphoglossoideae	Teratophyllum + Lomagramma	Genus	19	N	Wood et al. 2009/Liu et al. 2007/The Plant List/PalaeoDB
Elaphoglossoideae	Elaphoglossum	Genus	584	Y	Wood et al. 2009/Liu et al. 2007/The Plant List/PalaeoDB
Lomariopsidaceae	Cyclopeltis	Genus	3	N	Wood et al. 2009/Liu et al. 2007/The Plant List/PalaeoDB
Lomariopsidaceae	Lomariopsis	Genus	35	Y	Wood et al. 2009/Liu et al. 2007/The Plant List/PalaeoDB
Lycopodiaceae 1	Dendrolycopodium	Genus	4	N	Wood et al. 2009/Field et al. 2015/The Plant List/PalaeoDB
Lycopodiaceae 1	Diphasiastrum	Genus	21	Y	Wood et al. 2009/Field et al. 2015/The Plant List/PalaeoDB
Lycopodiaceae 2	Phylloglossum	Genus	1	N	Wood et al. 2009/Field et al. 2015/The Plant List/PalaeoDB
Lycopodiaceae 2	Huperzia	Genus	250	Y	Wood et al. 2009/Field et al. 2015/The Plant List/PalaeoDB
Lycopodiaceae 3	Pseudolycopodiella + Palhinhaea	Genus	10	N	Wood et al. 2009/Field et al. 2015/The Plant List/PalaeoDB
Lycopodiaceae 3	Lycopodiella	Genus	30	Y	Wood et al. 2009/Field et al. 2015/The Plant List/PalaeoDB
Lycopodiaceae 4	Spinulum	Genus	3	N	Wood et al. 2009/Field et al. 2015/The Plant List/PalaeoDB
Lycopodiaceae 4	Lycopodium	Genus	70	Y	Wood et al. 2009/Field et al. 2015/The Plant List/PalaeoDB
Marattiaceae	Angiopteris	Genus	75	N	Wood et al. 2009/Murdock 2008/The Plant List/PalaeoDB
Marattiaceae	Marattia	Genus	60	Y	Wood et al. 2009/Murdock 2008/The Plant List/PalaeoDB
Marsileaceae	Regnellidium + Pilularia	Genus	9	N	Wood et al. 2009/Nagalingum et al. 2007/The Plant List/PalaeoDB
Marsileaceae	Marsilea	Genus	111	Y	Wood et al. 2009/Nagalingum et al. 2007/The Plant List/PalaeoDB
Polypodiineae	Blechnoideae	Genus	246	N	Wood et al. 2009/Schuettpelz & Pryer 2007/The Plant List/PalaeoDB
Polypodiineae	Oleandraceae	Genus	80	Y	Wood et al. 2009/Schuettpelz & Pryer

					2007/The Plant List/PalaeoDB
Ophioglossaceae 1	Helminthostachys	Genus	6	N	Wood et al. 2009/Hauk et al. 2002/The Plant List/PalaeoDB
Ophioglossaceae 1	Botrychium + Botrypus + Sceptridium	Genus	132	Y	Wood et al. 2009/Hauk et al. 2002/The Plant List/PalaeoDB
Ophioglossaceae 2	Ophioderma + Cheiroglossa	Genus	16	N	Wood et al. 2009/Hauk et al. 2002/The Plant List/PalaeoDB
Ophioglossaceae 2	Ophioglossum	Genus	118	Y	Wood et al. 2009/Hauk et al. 2002/The Plant List/PalaeoDB
Cyatheales	Culcitaceae	Genus	6	N	Wood et al. 2009/Koral et al. 2006/The Plant List/PalaeoDB
Cyatheales	Plagiogyriaceae	Genus	20	Y	Wood et al. 2009/Koral et al. 2006/The Plant List/PalaeoDB
Polypodiaceae 1	Niphidium	Genus	14	N	Wood et al. 2009/Schneider et al. 2004/The Plant List/PalaeoDB
Polypodiaceae 1	Campyloneurum	Genus	74	Y	Wood et al. 2009/Schneider et al. 2004/The Plant List/PalaeoDB
Microsoreae	Leptochilus	Genus	114	N	Wood et al. 2009/Kreier et al. 2008/The Plant List/PalaeoDB
Microsoreae	Colysis	Genus	77	Y	Wood et al. 2009/Kreier et al. 2008/The Plant List/PalaeoDB
Drynarioideae	Polypodiopteris	Genus	3	N	Wood et al. 2009/Schneider et al. 2004/The Plant List/PalaeoDB
Drynarioideae	Selliguea	Genus	124	Y	Wood et al. 2009/Schneider et al. 2004/The Plant List/PalaeoDB
Polypodiaceae 2	Drymotaenium	Genus	1	N	Wood et al. 2009/Kreier et al. 2008/The Plant List/PalaeoDB
Polypodiaceae 2	Lepisorus	Genus	140	Y	Wood et al. 2009/Kreier et al. 2008/The Plant List/PalaeoDB
Polypodiaceae 3	Anarthropteris	Genus	2	N	Wood et al. 2009/Kreier et al. 2008/The Plant List/PalaeoDB
Polypodiaceae 3	Loxogramme	Genus	70	Y	Wood et al. 2009/Kreier et al. 2008/The Plant List/PalaeoDB
Polypodiaceae 4	Niphidium + Campyloneurum	Genus	74	N	Wood et al. 2009/Kreier et al. 2008/The Plant List/PalaeoDB
Polypodiaceae 4	Microgramma	Genus	38	Y	Wood et al. 2009/Kreier et al. 2008/The Plant List/PalaeoDB
Polypodiaceae 5	Lecanopteris + Leptochilus	Genus	130	N	Wood et al. 2009/Kreier et al. 2008/The Plant List/PalaeoDB
Polypodiaceae 5	Microsorum	Genus	118	Y	Wood et al. 2009/Kreier et al. 2008/The Plant List/PalaeoDB
Polypodiaceae 6	Calymmodon + Prosaptia + Grammitis + Themelium + Micropolypodium + Terpsichore + Adenophorus	Genus	590	N	Wood et al. 2009/Kreier et al. 2008/The Plant List/PalaeoDB
Polypodiaceae 6	Polypodium	Genus	1356	Y	Wood et al. 2009/Kreier et al. 2008/The Plant List/PalaeoDB

Platycerioideae	Platycerium	Genus	27	N	Wood et al. 2009/Kreier et al. 2008/The Plant List/PalaeoDB
Platycerioideae	Pyrrosia	Genus	109	Y	Wood et al. 2009/Kreier et al. 2008/The Plant List/PalaeoDB
Pteridaceae 1	Pteridoideae	Genus	1075	N	Wood et al. 2009/Schuettpelz et al. 2007/The Plant List/PalaeoDB
Pteridaceae 1	Ceratopteridoideae	Genus	322	Y	Wood et al. 2009/Schuettpelz et al. 2007/The Plant List/PalaeoDB
Pteridaceae 2	Sinopteris	Genus	3	N	Wood et al. 2009/Gastony & Rollo 1995/The Plant List/PalaeoDB
Pteridaceae 2	Aleuritopteris	Genus	63	Y	Wood et al. 2009/Gastony & Rollo 1995/The Plant List/PalaeoDB
Pteridoideae	Cosentinia	Genus	2	N	Wood et al. 2009/Schuettpelz et al. 2007/The Plant List/PalaeoDB
Pteridoideae	Anogramma + Pityrogramma	Genus	116	Y	Wood et al. 2009/Schuettpelz et al. 2007/The Plant List/PalaeoDB
Pteridaceae 3	Cheilanthes	Genus	375	N	Wood et al. 2009/Gastony & Rollo 1995/The Plant List/PalaeoDB
Pteridaceae 3	Argyrochosma + Pellaea + Platyloma	Genus	147	Y	Wood et al. 2009/Gastony & Rollo 1995/The Plant List/PalaeoDB
Pteridaceae 4	Cheilanthes	Genus	375	N	Wood et al. 2009/Gastony & Rollo 1995/The Plant List/PalaeoDB
Pteridaceae 4	Aspidotis	Genus	5	Y	Wood et al. 2009/Gastony & Rollo 1995/The Plant List/PalaeoDB
Pteridaceae 5	Llavea	Genus	1	N	Wood et al. 2009/Schuettpelz et al. 2007/The Plant List/PalaeoDB
Pteridaceae 5	Cryptogramma + Coniogramme	Genus	85	Y	Wood et al. 2009/Schuettpelz et al. 2007/The Plant List/PalaeoDB
Pteridaceae 6	Cheilanthes	Genus	375	N	Wood et al. 2009/Schuettpelz et al. 2007/The Plant List/PalaeoDB
Pteridaceae 6	Doryopteris	Genus	92	Y	Wood et al. 2009/Schuettpelz et al. 2007/The Plant List/PalaeoDB
Pteridaceae 7	Pterozonium + Taenitis	Genus	55	N	Wood et al. 2009/Schuettpelz et al. 2007/The Plant List/PalaeoDB
Pteridaceae 7	Jamesonia	Genus	60	Y	Wood et al. 2009/Schuettpelz et al. 2007/The Plant List/PalaeoDB
Pteridaceae 8	Adiantopsis + Cheilanthes + Doryopteris	Genus	504	N	Wood et al. 2009/Schuettpelz et al. 2007/The Plant List/PalaeoDB
Pteridaceae 8	Hemionitis	Genus	47	Y	Wood et al. 2009/Schuettpelz et al. 2007/The Plant List/PalaeoDB

Pteridaceae 9	Actiniopteris	Genus	8	N	Wood et al. 2009/Schuettpelz et al. 2007/The Plant List/PalaeoDB
Pteridaceae 9	Onychium	Genus	23	Y	Wood et al. 2009/Schuettpelz et al. 2007/The Plant List/PalaeoDB
Pteridaceae 10	Platyloma	Genus	1	N	Wood et al. 2009/Gastony & Rollo 1995/The Plant List/PalaeoDB
Pteridaceae 10	Pellaea	Genus	130	Y	Wood et al. 2009/Gastony & Rollo 1995/The Plant List/PalaeoDB
Pteridaceae 11	Ochropteris	Genus	2	N	Wood et al. 2009/Schuettpelz et al. 2007/The Plant List/PalaeoDB
Pteridaceae 11	Pteris	Genus	779	Y	Wood et al. 2009/Schuettpelz et al. 2007/The Plant List/PalaeoDB
Salviniaceae	Azolla	Genus	14	N	Wood et al. 2009/Nagalingium et al. 2008/The Plant List/PalaeoDB
Salviniaceae	Salvinia	Genus	29	Y	Wood et al. 2009/Nagalingium et al. 2008/The Plant List/PalaeoDB
Schizaeaceae 1	Actinostachys + Schizaea	Genus	85	N	Wood et al. 2009/Wikstrom et al. 2002/The Plant List/PalaeoDB
Schizaeaceae 1	Anemia + Mohria	Genus	185	Y	Wood et al. 2009/Wikstrom et al. 2002/The Plant List/PalaeoDB
Schizaeaceae 2	Microschizaea	Genus	7	N	Wood et al. 2009/Wikstrom et al. 2002/The Plant List/PalaeoDB
Schizaeaceae 2	Schizaea	Genus	56	Y	Wood et al. 2009/Wikstrom et al. 2002/The Plant List/PalaeoDB
Thelypteridaceae 1	Metathelypteris	Genus	19	N	Wood et al. 2009/Almeida et al. 2016/The Plant List/PalaeoDB
Thelypteridaceae 1	Amauropelta	Genus	23	Y	Wood et al. 2009/Almeida et al. 2016/The Plant List/PalaeoDB
Thelypteridaceae 2	Amphineuron	Genus	11	N	Wood et al. 2009/Almeida et al. 2016/The Plant List/PalaeoDB
Thelypteridaceae 2	Christella + Sphaerostephanos + Pronephrium	Genus	378	Y	Wood et al. 2009/Almeida et al. 2016/The Plant List/PalaeoDB
Thelypteridaceae 3	Ampelopteris + Mesophlebion	Genus	21	N	Wood et al. 2009/Almeida et al. 2016/The Plant List/PalaeoDB
Thelypteridaceae 3	Cyclosorus	Genus	526	Y	Wood et al. 2009/Almeida et al. 2016/The Plant List/PalaeoDB
Vittariaceae	Anetium	Genus	3	N	Wood et al. 2009/Crane 1995/The Plant List/PalaeoDB
Vittariaceae	Antrophyum + Polytaenium + Vittaria	Genus	242	Y	Wood et al. 2009/Crane 1995/The Plant List/PalaeoDB
Hymenophyllaceae	Vandenboschia	Genus	34	N	Wood et al. 2009/Ebihara et al. 2006/The Plant List/PalaeoDB

Hymenophyllaceae	Didymoglossum	Genus	75	Y	Wood et al. 2009/Ebihara et al. 2006/The Plant List/PalaeoDB

S2 List of Source Papers

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